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## CHARLES DARWIN AND THE MUTATION THEORY\*

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PROFESSOR HUGO DE VRIES, in his American lectures on "Species and Varieties, their Origin by Mutation," claims that his work is "in full accord with the principles laid down by Darwin,"<sup>1</sup> and boldly asserts that Darwin recognized both "mutation" and individual variation, or "fluctuation,"<sup>2</sup> as steps towards what Professor Cope aptly called "the origin of the fittest." I think many persons unfamiliar with Darwin's writings must have been much surprised on reading Professor De Vries's statement, for it has been a common belief in the scientific world for many years that the establishment of the mutation theory would be fatal to Darwinism, or would at least take from it its most original and essential features. The perpetuation of this impression has been due, very largely, to Mr. Wallace and certain of his followers who have steadfastly refused to admit the possibility of the evolution of species and varieties by any form of saltation and have insisted more uncompromisingly than did Mr. Darwin himself upon the exclusive efficiency of selection exercised upon small, recurring individual fluctuations. In fact, many of Mr. Wallace's views have out-Darwinized Darwin and yet Darwin, somewhat unreasonably, has been held responsible for them.

\* Presidential address at the annual meeting of the New York Academy of Sciences, December 21, 1908.

<sup>1</sup> Preface by the author, p. ix.

<sup>2</sup> Second edition, p. 7.

Accordingly Darwin has been charged with a radicalism which he never professed and champions of a *supposed* Darwinism have felt called upon to do battle against theories which he never distinctly repudiated or which he might even have accepted if he had known of them. Thus, Professor Poulton, in his recently published "Essays on Evolution," attacks with great severity, under the name of "Batesonians," believers in the validity of mutation as a factor in the process of evolution, although, as he admits, "mutation was of course well known to Darwin."<sup>3</sup> Now, I think we are justified in saying that if mutation was "*known*" to Darwin, it must have been, and still is, a veritable fact; and, if evolution is a universal law of nature it can not, in that case, exclude mutation. We, therefore, who believe in general evolution are compelled to decide for ourselves whether mutation has taken place and is now occurring; and we who are really Darwinians—that is to say, we who believe that Darwin set forth correctly the essential steps in the evolutionary process—are interested in knowing whether he actually recognized the fact of "discontinuous variation" or mutation, and, if so, how he fitted it into or reconciled it with his system.

The essential factors in organic evolution, from the Darwinian point of view, are: (1) Variation, (2) inheritance, (3) over-reproduction, (4) competition, (5) adaptation, (6) selection and survival. The general explanation of these factors is as follows:

1. All organisms vary continually and in every part of their structures—that is to say, no two individuals are exactly alike in any particular.
2. Nevertheless, characters anatomical, physiological and psychological are in general transmitted to descendants; in other words, progeny essentially resemble their parents.
3. More animals and plants are brought into the world than can possibly find means of subsistence.

<sup>3</sup> "Essays on Evolution," 1908, p. xviii.

4. There results competition for what subsistence there is, or, as it is otherwise called, a struggle for life.

5. Since out of all the variations that occur in the constitutions or characters of organisms some must happen to be in directions to give their possessors an advantage, or advantages, in procuring the means of existence, as compared with other individuals of the same class, some of the new-born animals and plants are best adapted to their surroundings or "conditions of life."

6. These best-adapted forms ("the fittest") will win in the struggle for life and are figuratively said to be selected; the unfit will in the end be exterminated. The result is the origination (evolution) of new classes of organisms out of the old ones and their substitution for the earlier classes or groups.

Not one of these factors was originally discovered by Darwin, but he first discerned their interrelations and bound them together by a consistent and convincing philosophy. He, for example, was not the earliest observer of progressive change in the organizations and external characters of animals and plants, but no one before him had had the insight to perceive that this changeability was the manifestation of a force great enough to burst the artificial limits placed about the groups called species and varieties and to enable them to transform themselves into other groups better adapted to the changing environment. Before Darwin's time every one, of course, had ocular demonstration of the fact that there were differences between individuals and that descendants were not in every respect like their ancestors. There was universal belief, however, that these variations never exceeded certain narrow boundaries built round species like inviolable walls. Curiously enough, Darwin, who first broke down these boundaries, took the same individual variations as the principal foundations of his selection theory. He assumed—for he admitted that it could not be proved for any particular case—that these small differences, which ordinarily fluctuate about a cer-

tain average for each species or variety, are at times accumulated to such a degree as to carry all the members of the group forward to a new center of oscillation so as to constitute in effect a new group. It was not at first his idea that a single individual, or a small number of individuals, might occasionally develop evolutionary force enough to over-leap suddenly the imaginary boundary and become the nucleus of a new colony beyond; that is the substance of the mutation theory; and, while I think it can be shown that Darwin more or less clearly recognized the possibility of the occasional origin of permanent races by this method of saltation, there can be no doubt that he entertained a strong bias in favor of the evolution of species generally by slow and minute steps.

As far as cultivated plants and domesticated animals were concerned Darwin was willing to grant the widest range of variation and the most abrupt changes, but as to animals and plants in a state of nature he was more sparing of his admissions that great and sudden departures from specific types might occur. This tenure of the two points of view was due to his belief that the domesticated animals and plants were more variable than feral forms because of the direct influence of man upon their surroundings and habits of life. Inasmuch as his theory of the origin of species through natural selection is founded on analogy between the deliberate operations of breeders in choosing the most desirable individuals of their flocks and gardens, and the inevitable sifting out of feral forms through their competition with one another in the struggle for existence, it is difficult to see why Mr. Darwin hesitated about carrying the comparison to its logical conclusion in the admission that what we now call mutations, but what he referred to as "spontaneous variations," "sports," "monstrosities," etc., stand upon substantially the same basis in nature as in cultivation. According to the present-day views of scientific students of animal and plant breeding, I understand, there is no

good evidence that cultivated plants and animals are more subject to wide and abrupt variations than are those living under natural conditions. On this point Professor De Vries remarks that "it is not proved, nor even probable, that cultivated plants are intrinsically more variable than their wild prototypes."<sup>4</sup> As to distinct mutations, we must remember that plants and animals preserved and nurtured by man are constantly under the eyes of many thousands of pecuniarily interested observers, while those in a state of nature are closely studied by but a handful of scientific investigators. We must also remember that it is only within a few years that a small fraction of these men of science have been led to look for cases of mutation, while all gardeners, farmers and breeders have had the inducement of financial profit to watch for marked variations among their stock and to preserve such variations if desirable. The naturalists specially interested in evolutionary questions are exceedingly few in number, but their field of research is immensely extended and varied. The number of those who have raised animals and plants for gain, however, has always been large, though the number of forms which they have been called upon to consider have been relatively few. The two fields have consequently had exceedingly different degrees of scrutiny. But since De Vries and others opened up the subject an astonishing number of clearly proven cases of mutation have been discovered in very various classes of organisms, just as numerous paleontological evidences of evolution have been brought to light as a consequence of Darwin's turning men's minds in that direction.

As I have already intimated, Mr. Darwin undoubtedly dealt with numerous cases of mutation among domesticated animals and plants, and they gave him little or no intellectual disquietude. In his work on "Animals and Plants Under Domestication" he gives a long catalogue of "spontaneous variations" or "sports," many of which

<sup>4</sup>"Species and Varieties, their Origin by Mutation," 2d ed., 1906, p. 66.

he freely acknowledges were the starting points of new and constant races; and there is good reason to believe that some of them occurred before the animals and plants which underwent the sudden changes had been actually brought under domestication or cultivation; in fact, that the mutations themselves suggested to men the directions in which their breeding operations should be conducted. For example, take the case of the tumbler pigeon: Mr. Darwin remarks concerning this that "no one would ever have thought of teaching or probably could have taught, the tumbler pigeon to tumble,"<sup>5</sup> but it seems to me obvious that no one would ever have thought of accumulating slight variations in the direction of tumbling. It is much more reasonable to suppose that the birds which were artificially selected as the progenitors of the present race of tumbler pigeons actually tumbled—that is to say, they were mutants. As to the origin of domestic races through modifications so abrupt as to have been thought by Darwin entirely independent of selection, he gave it as his judgment, as late as 1875, that

It is certain that the Ancon and Mauchamp breeds of sheep, and almost certain that the Niata cattle, turnspit and pug-dogs, jumper and frizzled fowls, short-faced tumbler pigeons, hook-billed ducks, &c. suddenly appeared in nearly the same state as we now see them. So it has been with many cultivated plants.<sup>6</sup>

Now, considering, as I said a moment ago, that Mr. Darwin's theory of the origin of species by means of natural selection has for its main foundation-stones facts derived from observation of the effects of man's selection among domesticated animals and plants,—without which, indeed, he admitted that he had no actual proof of the operation of natural selection,—it is difficult to realize the state of mind which led Mr. Darwin to add to the sentence just quoted the following caution:

The frequency of these cases is likely to lead to the false belief that natural species have often originated in the same abrupt manner. But

<sup>5</sup> "Origin of Species," 6th ed., 1882, p. 210.

<sup>6</sup> Ans. and Plnts. Under Dom., 2d ed., 1875, Vol. II, pp. 409–10.

we have no evidence of the appearance, or at least of the continued procreation under nature, of abrupt modifications of structure; and various general reasons could be assigned against such belief.

I am not aware that Mr. Darwin ever presented definite and convincing reasons for the sharp demarkation here attempted and, indeed, I can not see how the state of knowledge in his time could have justified it, for, as I have already stated, mutations had not been much looked for among feral plants and animals. In fact, by absolutely excluding from his theory the idea that mutation could occur under nature, Mr. Darwin, by the force of his great authority and influence, would have prevented a careful weighing of the pros and cons, if the human mind had at that time been prepared to weigh them. It is practically only since the Darwinian hypotheses have themselves been subjected to prolonged scrutiny, and since De Vries and a few others entered upon detailed experimental examination of this particular subject, within the last twenty years, that the matter can be said to have received anything like scientific treatment.

But, after all, Darwin was not *wholly* prejudiced against a belief in the occurrence of mutations in nature, for he several times expressed the opinion that the establishment of such a fact would in some ways be an advantage to the evolution theory. For instance, in a letter of August, 1860, to W. H. Harvey, he says:

About sudden jumps: I have no objection to them—they would aid me in some cases. All I can say is that I went into the subject and found no evidence to make me believe in jumps; and a good deal pointing in the other direction.<sup>7</sup>

This of course refers to discontinuous variations in organisms under natural conditions, for he had certainly found evidence to make him believe in similar variations among domesticated animals and plants. I think Mr. Darwin never specified the directions in which a belief in mutation would be a help to him, but, from casual remarks made in various places, I fancy he had in mind

<sup>7</sup> "More Letters," Vol. I, p. 166. See also, "Life and Letters," 1886, Vol. II, p. 333.

the way in which it would ease him over that difficult subject, the imperfection of the geological record, and would reconcile him with the physicists and cosmogonists who were not disposed to allow him the lapse of past time he required for the evolution of species by the accumulation of successive minute or "insensible" individual variations. But I will not discuss these points now. What I wish to dwell upon at the moment is that Darwin recognized and accepted the fact of mutation among animals and plants under domestication, although it is worth while to repeat the statement that some of his cases probably happened in a state of nature, since they occurred at the very beginning of, and were the points of origination for, man's selective operations. As Mr. Darwin himself says: "Man can hardly select, or only with much difficulty, any deviation of structure excepting such as is externally visible,"<sup>8</sup> which means, as I take it, that nature usually presents some quite manifest variation before artificial selection begins, and this must have been the case at the time when man's first choices were made, particularly when half-civilized and unobserving men began the cultivation of our now domesticated animals and plants. It is necessary to remember, however, in this connection, that the mutation theory, as interpreted by De Vries, requires for its starting point only a variation which marks a distinct separation of a form from its parent group without connecting gradations, and not necessarily any great or extraordinary change of characters; for, as he says: "Species are derived from other species by means of sudden small changes which, in some instances, may be scarcely perceptible to the inexperienced eye."<sup>9</sup> None the less it remains true that man is apt to select only striking variations and hence Mr. Darwin, in treating of "sports," or what we should now call mutants, among cultivated plants and animals, usually speaks of them as wide departures from type, or, rather, he deals only with such as are large deviations.

<sup>8</sup> "Origin of Species," 6th ed., p. 28.

<sup>9</sup> "Plant Breeding," 1907, p. 9.

Even when treating of organisms in a state of nature, however, he admits that "there will be a constant tendency in natural selection to preserve the most divergent offspring of any one species."<sup>10</sup> Returning to the subject of artificial selection, Mr. Darwin says:

No man would ever try to make a fan-tail till he saw a pigeon with a tail developed in some slight degree in an unusual manner, or a pouter till he saw a pigeon with a crop of somewhat unusual size; and the more abnormal or unusual any character was when it first appeared the more likely it would be to catch his attention.<sup>11</sup>

In another place he says:

It is probable that some breeds, such as the semi-monstrous Niata cattle, and some peculiarities, such as being hornless, &c. have appeared suddenly owing to what we may call, in our ignorance, spontaneous variation; . . . During the process of methodical selection it has occasionally happened that deviations of structure more strongly pronounced than mere individual differences, yet by no means deserving to be called monstrosities have been taken advantage of.<sup>12</sup>

Now, in his work on Animals and Plants under Domestication Darwin has given a long list of these widely varying forms from each of which has descended a new race conforming to his own test of a species, namely its possession of "the power of remaining for a good long period constant . . . combined with an appreciable amount of difference."<sup>13</sup> One of the most striking of these cases is that of the "japanned" or "black-shouldered" peacocks which have occasionally appeared "suddenly in flocks of the common kind," which "propagate their kind quite truly," which, according to good authority, "form a distinct and natural species," and which tend "at all times and in many places to reappear."<sup>14</sup> Mr. Darwin rejects the idea that these birds are the result of hybridization and reversion and declares in favor

<sup>10</sup> "Origin of Species," 6th ed., 1882, p. 413.

<sup>11</sup> *Ibid.*, p. 28.

<sup>12</sup> "Animals and Plants under Domestication," 2d ed., 1875, Vol. I, p. 96. See also, Vol. II, pp. 189-90.

<sup>13</sup> "More Letters of Charles Darwin," 1903, Vol. I, p. 252.

<sup>14</sup> "Animals and Plants under Domestication," 2d ed., 1875, Vol. I, pp. 305-7.

of their being "a variation induced by some unknown cause," and says that "on this view the case is the most remarkable one ever recorded of the abrupt appearance of a new form which so closely resembles a true species that it has deceived one of the most experienced of living ornithologists." In all points this case agrees with the modern idea of a mutation, even in the respect that it comes from a family of birds not usually considered very variable.

Concerning fowls Mr. Darwin remarks that

Fanciers, whilst admitting and even overrating the effects of crossing the various breeds, do not sufficiently regard the probability of the occasional birth, during the course of centuries, of birds with abnormal and hereditary peculiarities. Whenever, in the course of past centuries, a bird appeared with some slight abnormal structure, such as with a lark-like crest on its head, it would probably often have been preserved from that love of novelty which leads some persons in England to keep rumpless fowls and others in India to keep frizzled fowls. And after a time any such abnormal appearance would be carefully preserved from being esteemed a sign of the purity and excellence of the breed; for on this principle the Romans eighteen centuries ago valued the fifth toe and the white ear-lobe in their fowls.<sup>15</sup>

But Mr. Darwin's cases of what we must regard as saltations are not confined to the animal kingdom. We might easily cull from his list numerous more or less pertinent examples under the peach, plum, cherry, grape, gooseberry, currant, pear, apple, banana, camellia, crataegus, azalea, hibiscus, althaea, pelargonium, chrysanthemum, dianthus, rose and perhaps other plants. Concerning useful and ornamental trees he says: "All the recorded varieties, as far as I can find out, have been suddenly produced by one single act of variation,"<sup>16</sup> and as to roses, he remarks on their marked tendency to "sport" and to produce varieties "not only by grafting and budding, but often by seed," and quotes Mr. Rivers as saying that "whenever a new rose appears with any peculiar character, however produced, if it yielded seed" he "ex-

<sup>15</sup> "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 242-4.

<sup>16</sup> *Ibid.*, p. 384.

peets it to become the parent of a new family." In this connection Mr. Darwin called attention to the now well-known fact that the mutative tendency is an inheritable one by citing the case of the common double moss-rose, imported into England from Italy about the year 1735, which "probably arose from the Provence rose (*R. centifolia*) by bud-variation," the White Provence rose itself having apparently originated in the same way.<sup>17</sup> He also called attention to the significant fact that many abrupt variations were not to be attributed either to reversion or to the splitting-up of hybrids. Thus he declares:

No one will maintain that the sudden appearance of a moss-rose on a Provence rose is a return to a former state, for mossiness of the calyx has been observed in no natural species; the same argument is applicable to variegated and laciniated leaves; nor can the appearance of nectarines on peach-trees be accounted for on the principle of reversion.<sup>18</sup>

Further on in the same work he says:

Many cases of bud-variation . . . can not be attributed to reversion, but to so-called spontaneous variability, as is so common with cultivated plants raised from seed. As a single variety of the chrysanthemum has produced by buds six other varieties, and as one variety of the gooseberry has borne at the same time four distinct kinds of fruit, it is scarcely possible to believe that all these variations are due to reversion. We can hardly believe . . . that all the many peaches which have yielded nectarine-buds are of crossed parentage. Lastly, in such cases as that of the moss-rose, with its peculiar calyx, and of the rose which bears opposite leaves, in that of the *Imantophyllum*, &c., there is no known natural species or variety from which the characters in question could have been derived by a cross. We must attribute all such cases to the appearance of absolutely new characters in the buds. The varieties which have thus arisen can not be distinguished by any external character from seedlings. . . . It deserves notice that all the plants which have yielded bud-variations have likewise varied greatly by seed.<sup>19</sup>

Now, Darwin was here treating of saltations among cultivated plants, but it is instructive to read in this con-

<sup>17</sup> "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 405-6.

<sup>18</sup> *Ibid.*, Vol. II, p. 242.

<sup>19</sup> "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 439-40.

nexion the following passage in which he prepares the ground for a belief in the possibility of similar abrupt and wide variations under natural conditions. He remarks:

Domesticated animals and plants can hardly have been exposed to greater changes in their conditions of life than have many natural species during the incessant geological, geographieal, and climatal changes to which the world has been subject; but domesticated productions will often have been exposed to more sudden changes and to less continuously uniform conditions. As man has domesticated so many animals and plants belonging to widely different classes, and as he certainly did not choose with prophetic instinct those species which would vary most, we may infer that all natural species, if exposed to analogous conditions, would, on an average, vary to the same degree.<sup>20</sup>

But now let us take a specific example of spontaneous variability which deeply impressed Mr. Darwin. It is a case which was brought to his attention in 1860 by Professor W. H. Harvey concerning *Begonia frigida*, as to which Mr. Darwin says:

This plant properly produces male and female flowers on the same fascicle; and in the female flowers the perianth is superior; but a plant at Kew produced, besides the ordinary flowers, others which graduated towards a perfect hermaphrodite structure; and in these flowers the perianth was inferior. To show the importance of this modification under a classificatory point of view, I may quote what Professor Harvey says, namely, that had it "occurred in a state of nature, and had a botanist collected a plant with such flowers, he would not only have placed it in a distinct genus from *Begonia*, but would probably have considered it as the type of a new natural order." . . . The interest of the case is largely added to by Mr. C. W. Crocker's observation that seedlings from the *normal* flowers produced plants which bore, in about the same proportion as the parent-plant, hermaphrodite flowers having inferior perianths.<sup>21</sup>

This was written in the first edition of "Animals and Plants under Domestication" (1868) and was allowed to stand in the second and last edition (1875). In both editions, however, Mr. Darwin made the statement in an entirely different part of the work, that "the wonderfully anomalous flowers of *Begonia frigida*, formerly described, though they appear fit for fructification, are

<sup>20</sup> *Ibid.*, Vol. II, pp. 401-2. See also *ibid.*, Vol. II, p. 278.

<sup>21</sup> "Animals and Plants Under Domestication," 2d ed., Vol. I, p. 389.

sterile."<sup>22</sup> The last point, however, does not invalidate the claim to this new type of Begonia as a mutant, since the facts which determine its position in this regard are, first, the sudden appearance of the form bearing three kinds of flowers and, second, the production by seed of descendants also bearing three kinds of flowers.

It is very evident that this case troubled Mr. Darwin, for he referred to it a number of times and did not relish Professor Harvey's assertion that "such a case is hostile to the theory of natural selection, according to which changes are not supposed to take place *per saltum*," and Harvey's further declaration that "a few such cases would overthrow it (natural selection) altogether."<sup>23</sup> Sir Joseph Hooker attempted to explain the matter so as to weaken Professor Harvey's argument against the doctrine of natural selection, but Darwin himself wrote Hooker, saying:

As the "Origin" now stands Harvey is a good hit against my talking so much of the insensibly fine gradations; and certainly it has astonished me that I should be pelted with the fact that I had not allowed abrupt and great enough variations under nature. It would take a good deal more evidence to make me admit that forms have often changed by *saltum*.

About the same time, namely early in 1860, Darwin wrote to Lyell on this subject, saying:

It seems to me rather strange; he (Harvey) assumes the permanence of monsters, whereas monsters are generally sterile and not often inheritable. But grant this case, it comes that I have been too cautious in not admitting great and sudden variations.<sup>24</sup>

There is an added point of interest about this discussion in the fact that it is the earliest record in print of the consideration of saltation or mutation by Mr. Darwin.

You have doubtless noticed Mr. Darwin's protest against the belief in the occurrence of important changes "*per saltum*." He uses this expression with disapproval a number of times and yet his condemnation of

<sup>22</sup> *Ibid.*, 1st ed., Vol. II, p. 166. Also *ibid.*, 2d ed., Vol. II, p. 150.

<sup>23</sup> "Life and Letters," 1886, Vol. II, p. 274.

<sup>24</sup> *Ibid.*, p. 275. Also, "More Letters," 1903, Vol. I, p. 141.

the idea involved is not entirely unqualified, as is shown by the following significant statement:

On the theory of natural selection we can clearly understand the full meaning of the old canon in natural history, " *Natura non facit saltum.*" This canon, if we look to the present inhabitants alone of the world, is not strictly correct; but if we include all those of past times, whether known or unknown, it must on this theory be strictly true.<sup>25</sup>

This I understand to be in effect a protest against deducing proof of separate creations from the imperfection of the geological record, coupled with an admission that saltation or mutation does, at least occasionally, occur among existing living forms. I trust you perceive the importance of the concession that *natura non facit saltum* is not strictly correct as applied to *the present inhabitants of the world.*

Having noticed Mr. Darwin's repeated use of the words *per saltum*, I now wish to revert to his frequent use of the words *monster* and *monstrosity* and to call your attention to the fact that they are not always employed with exactly the same meanings. Sometimes by "monstrosity" he evidently intends to indicate a mere deformity of the nature of an accidental injury, or aborted or perverted development, but more generally he refers to a deviation from type wide enough, or discontinuous enough, to exclude it from the category of variations to which he supposed the operation of natural selection must be confined. Among domesticated animals and plants, however, the word *monster* as used by him often meant no more than the word "sport." In most cases when he used this term or one of its derivatives he took care to explain that monstrosities could not be qualitatively separated from other kinds of variations. Thus, in writing to R. Meldola, in 1873, he says:

It is very difficult or impossible to define what is meant by a large variation. Such graduate into monstrosities or generally injurious variations. I do not myself believe that these are often or ever taken advantage of under nature.<sup>26</sup>

<sup>25</sup> "Origin of Species," 6th ed., p. 166. See also *ibid.*, pp. 156, 234, 414.

<sup>26</sup> "More Letters," 1903, Vol. I, p. 350.

In the "Origin of Species" he wrote:

At long intervals of time, out of millions of individuals reared in the same country and fed on nearly the same food, deviations of structure so strongly pronounced as to deserve to be called monstrosities arise; but monstrosities cannot be separated by any distinct line from slighter variations.<sup>27</sup>

He frequently repeats this statement and it is quite clear that he intends to convey the idea that all variations are merely quantitative; at any rate he failed to adopt a nomenclature that would enable his readers to judge as to the degrees of difference he meant to indicate by such adjectives as "insensible," "minute," "slight," "large," "wide," "sudden" and "abrupt," as applied to variations. I am convinced, however, that he had in mind an idea that there were two different kinds of variations, namely, first, what he oftenest called "individual variations," by which he referred to the ordinary differences between the single organisms of the same group, or what mutationists now call "fluctuations," and, second, those radical and generally extensive deviations from type which constitute an actual break with the species, variety or race, and which are substantially what we of these later times have named "mutations." There are places in Darwin's works where the two kinds of variation just mentioned are spoken of as "indefinite" and "definite" and as results, respectively, of the *indirect* and the *direct* action of the conditions of life, and once only, I think, he uses the term "*fluctuating variability*" as synonymous with *indefinite variability*.<sup>28</sup> Now I do not assume to say that the recognition of these distinctions by Mr. Darwin proves that he clearly foresaw the present-day mutation theory with its foundation in the principle of unit characters, but I think it is true that he had at least a glimpse of the coming modifications

<sup>27</sup> "Origin of Species," 6th ed., p. 6, also p. 33. See also "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 312, 322. Also "More Letters," 1903, Vol. I, p. 318.

<sup>28</sup> "Animals and Plants Under Domestication," 2d ed., Vol. II, pp. 280, 281, 345.

to be required in his own theory to meet the then dawning truth. De Vries declares that his own field researches and testing of native plants are based "on the hypothesis of unit-characters as deduced from Darwin's Pangenesis," which conception, De Vries points out, "led to the expectation of two different kinds of variability, one slow and one sudden."<sup>20</sup>

But the main point I wish to dwell upon at present is that Darwin recognized, at least dimly, a kind of variability the results of which were essentially different from the "individual" or "indefinite" variations, which mistakenly seemed to him alone capable of being acted upon by selection. He was sorely puzzled by what he saw and realized in this direction, for he had spent more than twenty years of intense thought in elaborating his theory that new species were evolved from older ones by the gradual building up of new characters from extremely small differences, and he feared that the admission of saltation in any form meant the undermining of the foundations he had labored so hard to construct. He had once said:

When we remember such cases as the formation of the more complex galls, and certain monstrosities, which cannot be accounted for by reversion, cohesion, &c., and sudden strongly-marked deviations of structure, such as the appearance of a moss-rose on a common rose, we must admit that the organization of the individual is capable through its own laws of growth, under certain conditions, of undergoing great modifications, independently of the gradual accumulation of slight inherited modifications.<sup>21</sup>

In the last edition of the "Origin of Species," however, which was published in the year of the author's death, although he introduces this apology: "In the earlier editions of this work I underrated, as it now seems probable, the frequency and importance of modifications due to spontaneous variability,"<sup>22</sup> he still later inter-

<sup>20</sup> "Species and Varieties, their Origin by Mutation," 2d ed., 1906, p. 689.

<sup>21</sup> "Origin of Species," 5th ed., 1869, p. 151.

<sup>22</sup> "Origin of Species," 6th ed., 1882, p. 171.

polates the following rather sweeping recantation:

There are, however, some who still think that species have suddenly given birth, through quite unexplained means, to new and totally different forms; but, as I have attempted to show, weighty evidence can be opposed to the admission of great and abrupt modifications. Under a scientific point of view, and as leading to further investigation, but little advantage is gained by believing that new forms are suddenly developed in an inexplicable manner from old and widely different forms, over the old belief in the creation of species from the dust of the earth.<sup>22</sup>

In this sixth, and last, edition of the "Origin of Species" Mr. Darwin devotes to the task of answering criticisms made by St. George Mivart far more space than he had ever allowed to any other one critic and the passage just read is evidently one of those inspired by Mr. Mivart's attacks. The sore point with Mr. Darwin at that time was the doctrine of natural selection and, as I have already remarked, he had adopted the erroneous belief that this important principle must be greatly weakened if not entirely sacrificed if any form of saltation was to be admitted in nature. He had, therefore, wavered between his loyalty to his cherished hypothesis and his fearless devotion to truth. By this time, however, he had so long contemplated the possibility of the origin of new species and varieties through single long steps and had had so many convincing examples brought to his attention, that his hesitancy and doubt concerning the validity and sufficiency of the arguments urged in favor of this mode of evolution were ready to give way, and I regard the passage, which I am about to quote, as a virtual surrender on this point. The fact that, in this emphatic form, it was written at the close of his life, as his last word on this subject, and that he must have felt that it contained a concession very damaging to the theory to the establishment of which that life had been devoted, gives it, in my mind, a deeply pathetic significance. Mr. Darwin says:

<sup>22</sup> "Origin of Species," 6th ed., 1882, p. 424.

It appears that I formerly underrated the frequency and value of [variations which seem to us in our ignorance to arise spontaneously] as leading to permanent modifications of structure independently of natural selection. But as my conclusions have lately been much misrepresented, and it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work, and subsequently, I placed in a most conspicuous position—namely, at the close of the Introduction—the following words: "I am convinced that natural selection has been the main but not the exclusive means of modification." This has been of no avail. Great is the power of steady misrepresentation; but the history of science shows that this power does not long endure.<sup>33</sup>

The sting of this vehement declaration is in the underlying implication that the limitation placed upon the applicability of natural selection was deemed necessary because of Mr. Darwin's inability to free his mind from the belief that it could not act upon large and sudden variations as well as upon small and unimportant ones. This point of view seems illogical when we consider his repeated declaration that no qualitative distinction could be established between the two kinds of variation, but it may be partially accounted for by the fact that a slight confusion at times existed in his mind concerning the general *modus operandi* of natural selection, through which he attributed to it a *causal* power as well as a mere sifting effect. Both Lyell and Wallace took him to task for this double use of the term and, therefore, in the third edition of "the Origin" he attempted to clear up this point by means of this statement:

Several writers have misapprehended or objected to the term natural selection. Some have even imagined that natural selection even *induces* variability, whereas it implies only the preservation of such variations as arise and are beneficial to the being under its conditions of life.<sup>34</sup>

Nevertheless, almost side by side with this explanation we find in the last edition of "the Origin," the following sentences which were allowed to come down from the first edition: "Natural Selection will *modify* the

<sup>33</sup> "Origin of Species," 6th ed., p. 421. See also, "Life and Letters," 1886, Vol. III, p. 243, and "More Letters," 1907, Vol. I, p. 389.

<sup>34</sup> "Origin of Species," 3d ed., 1861, p. 84.

structure of the young in relation to the parent, and of the parent in relation to the young."<sup>35</sup> "Natural Selection . . . will *destroy* any individual departing from the proper type."<sup>36</sup> If Darwin had adopted the simile of a sieve, so effectively used by De Vries, he would have drawn nearer to the recognition of the fact of "selection *between* species," even if he had not been prepared to assent to De Vries's counter proposition that there is no "selection *within* the species." He might also have escaped some of his apprehensions concerning the fate of adaptation, which he thought to be endangered by a belief in saltation; for the fact is that adaptedness is only another name for fitness, and this is a quality inherent in the organism and precedent to selection—that is to say, natural selection merely sifts out for preservation the *adapted* or fit, allowing the unadapted or unfit to perish. Now, it is impossible to see why forms both adapted and unadapted to their environment may not arise through mutation and thus be offered to the operation of selection. In fact, Mr. Darwin has supplied us with a good illustration of such a case in a rather naïve passage which has run through every edition of "the Origin," to the following effect:

One of the most remarkable features in our domesticated races is that we see in them adaptation, not indeed to the animal's or plant's own good, but to man's use or fancy. Some variations useful to him have probably arisen suddenly, or by one step; many botanists, for instance, believe that the fuller's teasel, with its hooks, which can not be rivaled by any mechanical contrivance, is only a variety of the wild *Dipsacus*; and this amount of change may have suddenly arisen in a seedling.<sup>37</sup>

Surely, if Mr. Darwin could have looked at this case with a perfectly free mind, he must have perceived that the teasel's adaptation to man's needs would not have fallen if man had failed to exercise his power of selection; and that the adaptation was not weakened by the fact that it arose by a mutation. But that he was uncon-

<sup>35</sup> *Ibid.*, 6th ed., 1882, p. 67.

<sup>36</sup> *Ibid.*, 6th ed., 1882, p. 81.

<sup>37</sup> "Origin of Species," 6th ed., p. 22.

sciously biased in this matter is shown by an extract from a letter written to Asa Gray, in 1860, in which he says:

I reflected much on the chance of favorable monstrosities (*i. e.*, great and sudden variation) arising. I have, of course, no objection to this, indeed it would be a great aid, but I did not allude to the subject [*i. e.*, in "the Origin"] for, after much labor, I could find nothing which satisfied me of the probability of such occurrences. There seems to me in almost every case too much, too complex, and too beautiful adaptation, in every structure, to believe in its sudden production.<sup>38</sup>

The idea involved in this passage is that adaptation is *produced*—rather than *preserved*—by natural selection and that, as natural selection must, according to Mr. Darwin's curious prepossession, act only upon slow and small changes of character, adaptation itself must necessarily be in every case a matter of gradual growth. This sort of argument appears to justify the fear shared by both Lyell and Hooker that Darwin was at times disposed to stake his whole case on the maintenance of an unnecessary assumption. Hooker wrote him as early as 1859 or 1860 that he was making a hobby of natural selection and overriding it, since he undertook to make it account for too much.<sup>39</sup> Darwin mildly protested that he did not see how he could do more than he had done to disclaim any intention of accounting for everything by natural selection.<sup>40</sup> In this discussion; however, it is apparent that while Darwin was overloading the theory of natural selection with a responsibility for the origin of the adapted or fit, he was at the same time unduly limiting it to only one class of the fit, namely those which had arisen by slow degrees. If he had taken the position that natural selection could and would operate upon any kind or any degree of variability, he need not to have imagined that his main doctrine was in jeopardy.

But though Mr. Darwin could be stirred by attack to a vigorous defense, and sometimes even to an *over-defense*, of natural selection, he contended, at other times, with equal vigor, that his main interest was with varia-

<sup>38</sup> "Life and Letters," 1887, Vol. II, p. 333.

<sup>39</sup> "More Letters," 1903, Vol. I, p. 135.

<sup>40</sup> *Ibid.*, Vol. I, pp. 172, 213.

tion, however produced, which was the necessary basis of the whole evolutionary process. He admitted, however, that the cause of variation was to him inexplicable and, like all beginnings, it remains to this day a deep mystery. Darwin said of it:

Our ignorance of the laws of variation is profound. Not in one case out of a hundred can we pretend to assign any reason why this or that part has varied.<sup>41</sup>

In another place he remarks:

When we reflect on the millions of buds which many trees have produced before some one bud has varied, we are lost in wonder as to what the precise cause of each variation can be.<sup>42</sup>

He never definitely undertook to solve this mystery, though he reflected and reasoned on it much. The nearest he came to formulating a law concerning it was the expression of his conviction that variability was more a matter of organic constitution than a result of external agencies. Thus he declares:

If we look to such cases as that of a peach tree which, after having been cultivated by tens of thousands during many years in many countries, and after having annually produced millions of buds, all of which have apparently been exposed to precisely the same conditions, yet at last suddenly produces a single bud with its whole character greatly transformed, we are driven to the conclusion that the transformation stands in no *direct* relation to the conditions of life.<sup>43</sup>

From examples like this Mr. Darwin deduced a "general rule that conspicuous variations occur rarely, and in one individual alone out of millions, though all may have been exposed, as far as we can judge, to nearly the same conditions"<sup>44</sup> and while this is, in a general way, in accordance with the admission of De Vries that although mutations are "not so very rare in nature,"<sup>45</sup> the numbers "under observation are as yet very rare,"<sup>46</sup> we shall see a little later that Mr. Darwin's deduction is not

<sup>41</sup> "Origin of Species," 6th ed., p. 131.

<sup>42</sup> "Animals and Plants Under Domestication," 2d ed., Vol. II, p. 281.

<sup>43</sup> *Ibid.*, 2d ed., Vol. I, p. 441. See also, *ibid.*, Vol. II, pp. 277, 279, 282.

<sup>44</sup> "Animals and Plants Under Domestication," 2d ed., Vol. II, p. 276.

<sup>45</sup> "Species and Varieties, their Origin by Mutation," 2d ed., p. 597.

<sup>46</sup> *Ibid.*, p. 8.

strictly accurate since it excludes the idea of a whole genus or species or variety mutating at once.

While on this subject, I may mention that Mr. Darwin anticipated the doctrine of the mutationists to the effect that "when the organization has once begun to vary, it generally continues varying for many generations."<sup>47</sup> But as to variability having periods of activity Mr. Darwin's opinion seems to have been unsettled. In a letter to Weismann, in 1872, he remarks on the strangeness "about the periods or endurance of variability,"<sup>48</sup> but in a letter to Moritz Wagner, in 1876, he says:

Several considerations make me doubt whether species are much more variable at one period than at another except through the agency of changed conditions. I wish, however, that I could believe in this doctrine, as it removes many difficulties.<sup>49</sup>

Practically this is the dilemma of the mutationists of the present day: they are not in a position to prove that plants and animals have periods of mutation, but they assume that it must be so, because the belief "removes many difficulties."

One of Darwin's perplexities, however, has been explained away, as I have already pointed out, by the discovery that mutation is not confined to a single case out of millions of individual forms, nor even to a single generation out of a long genetic line, but that, as in the case of the *Oenotheras* (evening primroses), a whole genus is likely to be in a mutating condition at the same time, producing from each of several species numberless individual mutants, which are themselves often in a mutating condition, the parent stock meanwhile remaining perfectly constant. Such has been the case with *Oenothera (Onagra) lamarckiana*, which, while throwing off, since it has been under scientific observation, in large numbers not less than a dozen elementary species and retrograde varieties, has bred true to its original type through at least one hundred and sixteen years, although there is

<sup>47</sup>"Origin of Species," 6th ed., p. 5.

<sup>48</sup>"Life and Letters," 1886, Vol. III, p. 155.

<sup>49</sup>*Ibid.*, p. 158.

considerable proof that it is itself a mutant from *Oenothera grandiflora*, and none whatever for the assertion, often made, that it is a hybrid. As at least nine of its mutants have also bred true through many generations in pedigree cultures and doubtless had been constant forms for a long time in a state of nature, there appears to be no ground for Darwin's fear that, granting the occurrence of mutation, the mutants would be liable to speedy extermination through inability to propagate. Of course this would not be the case with even a single self-fertilizing plant and it would not be true with animal mutants if, like plant mutants, they were produced in numbers by the mutating stock. As to swamping by intercrossing, it has been shown that, under Mendel's law, in the extreme case of the production of a solitary mutant obliged to cross with the parent form, if it possesses characteristics having a certain relation to the parent, it can establish a race like itself and even supplant the parent form, if it is only *as well* fitted for the battle of life as is the progenitor.<sup>50</sup>

If Darwin had known these facts he would not have written, or he would have greatly amended, the following passage:

He who believes that some ancient form was transformed suddenly through an internal force or tendency into, for instance, one furnished with wings, will be almost compelled to assume, in opposition to all analogy, that many individuals varied simultaneously. It can not be denied that such abrupt and great changes of structure are widely different from those which most species apparently have undergone. He will further be compelled to believe that many structures beautifully adapted to all the other parts of the same creature and to the surrounding conditions, have been suddenly produced; and of such complex and wonderful co-adaptations, he will not be able to assign a shadow of an explanation. He will be forced to admit that these great and sudden transformations have left no trace of their action on the embryo. To admit all this is, as it seems to me, to enter into the realms of miracle, and to leave those of science.<sup>51</sup>

Of course Mr. Darwin was not entirely oblivious to the fact that every important advance in knowledge must

<sup>50</sup> See Lock's "Variation, Heredity and Evolution," 1906, p. 205.

<sup>51</sup> "Origin of Species," 6th ed., p. 204. See also, *ibid.*, p. 202.

have the appearance, at first, of a moye into a region of mystery and uncertainty. The lapse of time and the growth of familiarity with it are necessary to the reclamation of a *terra incognita*.

Before leaving this branch of my subject, I desire to call your attention to the very interesting fact that Mr. Darwin himself once conducted a long series of experiments which, it can hardly be doubted, resulted in the production of mutants and that he just missed the discovery of principles which are now the basis of scientific pedigree cultures and are occupying the attention of investigators of the problems of variation and heredity. In a letter to J. H. Gilbert, dated February 16, 1876, Mr. Darwin writes:

Now, for the last ten years I have been experimenting in crossing and self-fertilizing plants; and one indirect result has surprised me much, namely, that by taking pains to cultivate plants in pots under glass during several successive generations, under nearly similar conditions, and by self-fertilizing them in each generation, the colour of the flowers often changes, and, what is very remarkable, they became in some of the most variable species, such as *Mimulus*, *Carnation*, &c., quite constant, like those of a wild species. This fact and several others have led me to the suspicion that the cause of variation must be in different substances absorbed from the soil by these plants when their powers of absorption are not interfered with by other plants with which they grow mingled in a state of nature.<sup>22</sup>

The point I particularly wish you to notice in this case is that Mr. Darwin was employing practically the methods now used by Professor De Vries, Professor MacDougal and others who are engaged in species testing, by growing naturally variable or mutating plants under conditions of rigid control, so as to exclude crossing or, as De Vries calls it, *vicinism*. In this view of the matter, it would be interesting to know what percentage of Mr. Darwin's plants exhibited the new and constant characters and through how many generations his mutants were found to breed true, for then we could compare his results with those of investigators of our day. But his attention was centered upon the endeavor to find a cause

<sup>22</sup> "Life and Letters," 1886, Vol. III, p. 343.

for the abrupt variations and not on the formulation of laws of their action. Apparently he considered isolation to be the principal secondary cause or favoring condition, upon which view the obvious comment is that it requires no great stretch of imagination to conceive of similar isolation as occurring in nature and thus favoring mutation among uncultivated forms.

Having now hastily reviewed the oscillations in Darwin's opinions concerning the kinds, the causes and the laws of variation with relation to the origin of species, it is not my purpose to enter upon a discussion of the present-day mutation theory, which has grown out of a closer study, and a more scientific treatment, of the problems of variation and heredity than were attempted, or were perhaps possible in Darwin's time. It is desirable, however, to compare Darwin's views with generalizations from the mutation theory, which we can do, well enough for our present purpose, by merely recalling the seven laws which De Vries claims to be the logical outcome of his twenty years of cultural experiments upon plants. They are, with slight modifications as to wording and order, as follows:

1. New elementary species appear suddenly without intermediate steps.
2. New forms spring laterally from the main stem.
3. New elementary species attain their full constancy at once.
4. Some of the new strains are elementary species, while others are to be considered as retrograde varieties.
5. The same new species are produced in a large number of individuals.
6. Mutations take place in nearly all directions and are due to unknown causes.
7. Species and varieties have originated by mutation, but are, at present, not known to have originated in any other way.

Now, looking back over what Darwin wrote concerning variation, I can not believe that he would seriously have

disputed any of De Vries's propositions except the last. All would have had to stand or fall with that. He recognized the fact that new species had sometimes appeared suddenly without intermediate steps and that the new forms had sprung laterally from the main stem. I think he also substantially admitted that such new species attained their full constancy at once. As to the fourth affirmation of De Vries, with reference to elementary species and retrograde varieties, Darwin had no knowledge, for the distinction is original with De Vries. Darwin believed, as a general proposition, that "species are only strongly marked and permanent varieties, and that each species first existed as a variety,"<sup>53</sup> but, of course, in admitted cases of mutation this can not be true; and if Darwin had been obliged to concede De Vries's seventh proposition, the fourth might well have been allowed to go with it. The same is doubtless the case concerning De Vries's fifth law, which sets forth in effect that similar mutants are thrown off by many individuals of the same species at about the same time. As we have already seen, Mr. Darwin was convinced that if, for example, he were to admit the origin by mutation of a species of flying animal, for the reasons urged by Mr. Mivart, he would be compelled to assume "that many individuals varied simultaneously." I, therefore, do not see that he would have been interested, from a theoretical point of view, in disputing either of the two last-named declarations of De Vries except in connection with his seventh and last law, to which I shall presently refer. The sixth law of De Vries, which affirms that mutations take place in nearly all directions, is practically the equivalent of Darwin's first law that all organisms vary continually and in every part of their structure, provided it is agreed that mutations are only quantitatively different from Darwin's "individual variations," which was Darwin's own view. In so far as Darwin admitted the occurrence of mutation at all, he must have agreed that it could proceed in any

<sup>53</sup> "Origin of Species," 6th ed., 1882, p. 412.

direction. But now we come to the conclusion of De Vries which we know Darwin would not have accepted, at least in its entirety. As we have seen, he was compelled to concede that what we now call mutation had occasionally taken place and become the starting point of new races, but he was none the less unshaken in the conviction that this process was exceptional and extraordinary, and that, as a rule, a new species originated by the gradual building up of minute and even insignificant deviations from the average characters of an old species, which deviations we now call fluctuations. We know with what tenacity he held this view to the end of his life. For the doctrine of "insensible gradations," which touched mainly a minor premise in his general argument for evolution, Mr. Darwin was, unhappily, almost willing to relinquish the essence of the whole matter, which was his claim to the discovery of a *vera causa* in the evolutionary process. Notwithstanding the prior claim of Patrick Matthew, and the partial anticipation of Alfred R. Wallace and others, the establishment of the theory of natural selection was Mr. Darwin's most original and greatest achievement. Time has proved that he could have afforded to stand upon the general validity and applicability of this theory though every step in his argument in its favor had needed review and modification; for each passing year but adds to the impregnable mass of proofs by which it is affirmed and supported. Properly regarded, the mutation theory does not antagonize nor weaken the doctrine of natural selection—on the contrary, it merely offers itself as a helpful substitute for, or adjunct to, one of Darwin's subordinate steps in the approach to a consistent philosophy of the origin of species, leaving the last great cause of evolution as efficient as ever. It is, therefore, one of the tragedies of science that in this matter Darwin should have been ready to surrender his main position rather than to receive and to join forces with those who were coming to his aid, but whom he failed to recognize as friends.

## JUVENILE KELPS AND THE RECAPITULATION THEORY. II

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### II. THE RECAPITULATION THEORY IN RELATION TO THE KELPS

ANY observations on juvenile kelps must call to mind the recapitulation theory. This theory, though applied both to animals and to plants, was built up exclusively on zoological evidence and has been amplified and discussed chiefly by zoologists. The reason is evident because of the definite proportions and structure of the animal body, the development of which must of necessity follow a very definite course, while among plants the body is of such loose and indefinite proportions that its development can seldom be rigidly described. But while the botanists have had very little to say about the recapitulation theory, they have always approved it and considered that it applied to plants just as truly, though not as conspicuously, as to animals.

It is somewhat surprising then to a botanist to find that this theory is being very vigorously attacked by some of the zoologists. One of the more recent papers is by Montgomery, who gives a review of the literature with a general discussion of the theory in his "Analysis of Racial Descent," 1906. In summing up he says (p. 193) :

Therefore we can only conclude that the embryogeny does not furnish any recapitulation of the phylogeny, not even a recapitulation marred at occasional points by secondary change. . . . An analysis of the stages during the life of one individual can in no way present a knowledge of its ancestry; and the method of comparing non-correspondent stages of two species is entirely wrong in principle.

And again at the close of the chapter, p. 203:

The recapitulation hypothesis is scientifically untenable and where there has been transmutation of species, the embryogeny neither in

whole nor in part exactly parallels the racial history. The relation between them is always that of an inexact parallelism. Considerations based on any such idea of recapitulation are erroneous, and therefore of no help in determining racial descent.

In these sentences Montgomery is voicing not alone his individual opinion, but that of a very considerable school of embryologists.

The general tenor of these statements is scarcely open to question nor is the author's conclusion as to the worthlessness of the recapitulation theory. However, there is one word used in both the paragraphs quoted, though not in the portion of the first cited, that is unfortunate in that it is open to misunderstanding. It is the word exact. Exact has a certain mathematical flavor, which makes its application to living organisms difficult. Neither Montgomery nor any one else believes that there are anywhere two individuals, who are exactly alike in any respect whatever. We may fairly assume, that Montgomery means to say that there is no recapitulation of the racial history of the embryo sufficiently exact to aid in determining racial descent; and we shall so interpret his statements in the remainder of this paper.

A few years ago when the recapitulation theory was almost universally accepted one might have assumed that the noteworthy features of the development of the kelps were to be explained on that basis. But now in the face of such attacks on the theory no such assumption may be made. We shall therefore consider the development of the kelps in relation to the theory and to the criticism upon it in an effort to ascertain the real bearing of the foregoing observations.

It must be admitted that the juvenile forms of all the kelps are closely similar in a general way; but it does not necessarily follow that they are so because of any recapitulation of phylogeny. Such parallelism might be brought about by entirely different causes. This possibility has been perhaps most strongly urged by His, the eminent embryologist, who in a different way makes quite as

strong an attack on the theory as does Montgomery. In his "Unsere Körperform" as translated and quoted by Morgan ('03, p. 71) who does not, however, assent, His says:

In the entire series of forms which a developing organism runs through, each form is the necessary antecedent step of the following. If the embryo is to reach the complicated end forms, it must pass, step by step, through the simpler ones. Each step of the series is the physiological consequence of the preceding stage and the necessary antecedent for the following. Jumps, or short cuts, of the developmental process, are unknown in the physiological process of development. If embryonic forms are the inevitable precedents of the mature forms, because the more complicated forms must pass through the simpler ones, we can understand the fact that paleontological forms are embryonal, because they have remained at the lower stage of development, and the present embryos must pass also through lower stages in order to reach the higher. But it is by no means necessary for the later, higher forms to pass through embryonal forms because their ancestors have once existed in this condition. To take a special case, suppose in the course of generations a species has increased its length of life gradually from one, two, three years to eighty years. The last animal would have had ancestors that lived for one year, two years, three years, etc., up to eighty years. But who would claim that because the final eighty years species must pass necessarily through one, two three years, etc., that it does so because its ancestors lived one year, two years, three years, etc.? The descent theory is correct in so far as it maintains that older, simpler forms have been the forefathers of later, complicated forms. In this case the resemblance of the older, simpler forms to the embryos of later forms is explained without assuming any law of inheritance whatever. The same resemblance between the older and simpler adult forms would remain intelligible were there no relation at all between them.

There are two ways of looking at this view of His's that every form is the necessary antecedent of the succeeding. These depend upon the length of stages considered. If we take stages separated by very small intervals of growth, His's contention must be true else there would be no continuity of development. But this is nothing more than a statement of the fact that all growth must be gradual and is no law of development. If instead of small intervals we take the whole development, the statement

would become: "The developmental stages of an organism are only the physiologically necessary steps for the formation of its adult body from its earliest stage, which is in most cases the egg." This is definite and it can be readily tested by the facts, while the other is so vague as to be scarcely susceptible of any such test. There is no middle ground between these two alternative interpretations of the statement. For if an organism is found to which it will not apply if somewhat but not greatly separated stages be considered, all that is necessary is to take shorter and shorter stages until finally any ontogeny must conform to it.

Let us apply then, His's view, thus interpreted, to the kelps. We have so far confined the account to the external morphology and have said little about their histology. This will be of interest here. The general plan of structure is the same in both stipe and lamina and similar in all kelps. Within the epidermis is the cortex composed of polygonal or rounded cells which may be thickened and hardened to form strengthening tissue. Within this is a pithweb made up of irregularly interlacing filaments which sometimes show very remarkable differentiation. Oliver ('87) first worked out in detail, showing that in *Macrocystis* and *Nereocystis*, especially, sieve tubes are developed which form a regular zone of vertical vessels around the less differentiated center of the pith. The sieve plates of these become obliterated by the formation of callus as in the spermatophytes. There is good reason to believe that they are efficient in the transfer of materials from one part of the plant to another and their possession may have made it possible for these plants to attain the great lengths they sometimes reach. The simpler internal pith consists of interlacing branching hyphae which run in all directions. Many of these meet and at their junctures develop sieve plates connecting them with one another, at the same time becoming swollen at the ends like the flare of a trumpet. Such trumpet hyphae are common in most members of the Laminariaceae. In Ren-

frewia, however, the pith consists of only moderately elongated cells which interlace somewhat as in other kelps, but very much less conspicuously. The majority of them are not longitudinal, but transverse in their general course, so that a cross section shows more of them cut lengthwise than a longitudinal (see figures, Griggs, '06). Scarcely any of them are sufficiently elongated to merit the name of hyphae. Very few give indications of developing into trumpet hyphae. It is evident that Renfrewia presents a transition from a pithweb of simple polygonal cells to the complex differentiation of the higher kelps such as *Nereocystis*. Such plants must of necessity pass through the condition of Renfrewia in order to attain mature structure. We have here then a perfect illustration of the truth of His's idea—save in one respect. His contends that the developmental stages are *only* the necessary morphological precursors of the adult. But in this case they may be phylogenetic recapitulations also. There is nothing in the evidence so far to prevent a decision either way.

Let us consider some other features of the development. All of the young forms pass through a period when the stipe is short as compared with the lamina. In all which have been described above except *Hedophylum*, this condition persists until a certain very definite period, after which the stipe elongates rapidly (see figures of *Egregia*). This condition is so similar to the adult stage of Renfrewia that one is tempted to consider it a recapitulation of such a stage. But instead it may be only a necessary physiological adaptation which the young plant undergoes early in its development in order to provide a large photosynthetic area to furnish the food necessary for rapid growth. *A priori* this would seem a reasonable interpretation of the facts and it may be that we should consider them without other significance. It is, however, difficult to believe that the simple Renfrewioid form is the necessary precursor of adult forms so diverse as *Postelsia* and *Egregia*, *Eisenia* and

*Nereocystis*, *Thallasiophyllum* and *Macrocytis*. One might imagine other forms upon which each of these might have been built up more directly than on this one. This is particularly true in the case of *Egregia* and *Hedophyllum*, where, while the young are indistinguishable, the course of development is diametrically opposed. *Egregia* dwarfs the lamina and becomes nearly all stipe; *Hedophyllum* obliterates the stipe and becomes a sessile lamina. If ontogeny represents merely stages physiologically necessary to the attainment of the adult form, why should *Hedophyllum* produce a stipe at all?

Similar conditions are presented by very many other cases, especially among animals where some organ is developed in the embryo which later disappears without being of service either to the embryo or to the adult. Such cases have in the past been the main evidence brought forward for the recapitulation theory, as it has been supposed they were explicable only on the basis of a recapitulation of the phylogeny. Familiar examples are cited by Morgan (see below), and many more might be added.

Not all who attack the recapitulation theory go so far as to discard it altogether. Many recognize in it a truth and seek to modify it to fit certain facts. The form which has the largest number of adherents is perhaps that proposed by Morgan ('03), who believes that animals in their ontogeny repeat not the adult, but the embryonic stages of their ancestors; that the presence of a certain structure in the embryo means that the ancestors of the species to which the organism belongs had similar embryonic stages. This he calls the "Repetition Theory." Much of the evidence which the zoologists bring forward in favor of such a modification as against any broader application is so conclusive, one must acknowledge that such is a correct statement of the facts in the particular cases cited, whatever the general law of development may be. Morgan calls attention to the fact that the gill-clefts and the notochord, structures on

the recurrence of which the recapitulation theory was largely built, appear just as early in the embryo of the fish and of *Amphioxus*, respectively, as in that of a mammal. He cites the case of the baleen whale which forms teeth in the embryo like any other mammal, but these beginnings, instead of continuing their development, are absorbed and do not even pierce the gums. The same is true of the dental ridges of birds, where teeth begin to form but soon disappear.

The evidence presented by the kelps clearly tends to establish this repetition theory of Morgan. The juvenile forms of the plants have so many points in common that there can be scant doubt but that their ancestors had similar juvenile forms. It must be added here also that those plants whose development we have traced above are not special cases, but are only illustrations of the facts common to all kelps. The writer has in his possession full series of several genera which have never been described at length. These and all others which have been worked out follow the same course of development. Among those upon which fairly complete published data are available, may be mentioned: *Agarum*, Barber, '89; *Alaria*, Schrader, '03, and others; *Cymathere*, Griggs, '07; *Eisenia*, Setchell, '96b, '05a; *Lessonia*, Reinke, '03; *Nereocystis*, MacMillan, '99; *Pterygophora*, MacMillan, '02; *Saccorhiza*, Barber, '89; *Thallasiophyllum*, Setchell, '05a.

If we may consider the repetition theory established how much will it help us with our phylogenetic problem? Why should widely diverse forms have ancestors with similar embryos? How were these similar stages acquired and why do they persist? They must be meaningless so far as phylogeny is concerned, except as they are considered as stages which once led to the development in the adult of the structures which they represent. But why should embryonic characters persist and not adult ones? Is there any line of demarkation between embryo and adult beyond which the action of heredity changes?

Leaving these questions for the present, we may examine the facts in the development of our kelps, to ascertain whether these juvenile forms repeat only other juvenile forms or whether they go farther and approximate the adults of their ancestors. Nothing could be more instructive on this point than the figure of the young plant of *Lessoniopsis* printed beside the adults of *Renfrewia* (Figs. 15-17). In all external characters save the characteristic spots of *Lessoniopsis* and the reproductive maturity of *Renfrewia* they are in essentials identical. The structure of the holdfast is particularly interesting. Both are simple discs strengthened by primary hapteres originating through the uneven growth of the disc itself. The young of other kelps might have been used for this comparison, *e. g.*, *Hedophyllum* (*cf.* Fig. 6), but *Lessoniopsis* retains these primitive characters at a larger size than the others and therefore lends itself more easily to photography while its determination is at the same time certain because of the spotted lamina. In *Pterygophora* the correspondence is in all respects just as complete, see MacMillan's figures ('02). There persists for a considerable period the simple lamina with the short stipe on the primitive disc and its primary hapteres for holdfast. After the secondary hapteres have appeared and until the midrib has been formed the young plants are very difficult to distinguish from those of *Laminaria saccharina* which grows in the same locality. These again are in all respects, except size and reproductive maturity, like the adult plants of their species.

It seems obvious that we can not well consider these facts without comparing these non-correspondent stages of *Lessoniopsis* and *Renfrewia*, and of *Pterygophora* and *Renfrewia* and *Laminaria*. The simple facts of the case are that *Lessoniopsis* and the others when still very small pass through a condition which must be considered within the generic limits of *Renfrewia*. Conversely, the adults of *Renfrewia* do not differ in any important char-

acters save size and reductive maturity from the young of the other kelps which have been studied. But Renfrewia, juvenile or adult, is not one of the ancestors of these higher kelps. It is only a simpler form which we take to have been left behind in the evolution of the kelps. Our actual knowledge of their ancestors is almost nothing. But if we were to reconstruct a generalized common ancestor for the kelps, by projecting backward, from the different tribes, lines indicating their apparent course of evolution, until they converged and met, we should have to conceive a plant very similar in all respects to Renfrewia.

What then is to be said concerning structures which do not recapitulate adult but only embryonic conditions? In the toothless animals, the whale and the bird, the development of teeth in the jaw is entirely unnecessary, as has been pointed out in considering His's idea. It may even be said to hinder the attainment of the adult condition. The same is true of the mammalian gill-slits and of most of the structures which have in the past attracted attention in connection with the recapitulation theory. As the ancestral period, when such structures were fully developed in the adult, becomes more and more remote, the tendency to inherit them becomes less and less, because of the cumulative impulses given to the heritage by the nearer ancestors. Consequently, they are successively less and less developed. Any gradual loss of inherited structures can, in the nature of the case, take place only from the mature condition backward towards the beginning of the life cycle; otherwise we should have adult structures with no ontogenetic history. Therefore we can understand why it is that in many cases only the embryonic stages of ancestral organs persist in the ontogeny.<sup>3</sup>

<sup>3</sup>The cutting off of end stages in the development of organs has given rise to the idea that the adult stages are "pushed back into the embryo." Such a misconception easily arose from the loose language in which the facts have often been expressed. Conklin ('05) has rightly pointed out its incorrectness.

Thus the embryogeny will be gradually shortened by the omission of more and more of the superfluous ancestral stages; and it will tend finally to retain only such stages as are necessary to the attainment of the adult form. It will be noted that this is the view of His, which thus becomes a statement of an inevitable tendency in development, which is very different from a complete law of embryogeny. Though life cycles may approach very closely such a limiting condition, it is doubtful if they would ever completely realize it.

Besides changes in ontogenies brought about by the cutting off of end stages no longer used there is another source of change. This is secondary adaptation. It is on this point that Montgomery largely makes his case, insisting that organisms are as subject to change in one period of their life cycles as another. In this matter also we must agree that secondary changes are sometimes very evident and conspicuous—probably more so among animals than plants. The fetal membranes are very familiar examples of such secondary adaptations. But though they are much modified the fact must not be lost sight of that they are in part at least adaptations of previously existing organs with different functions and not new structures. Not only may an embryo adapt itself to its conditions; it may simulate other forms; or interpolate stages; or become otherwise modified as the species undergoes transmutation. Yet the important point to consider is not that a few have done this, but that the great majority have not falsified their heritage beyond all recognition, that they still persist in spite of changed conditions and secondary adaptation in preserving so many indications of their ancestry.

Montgomery considers this matter of secondary change so weighty, not because of a great amount of observation brought forth, but for logical reasons. He holds that:

The egg of a mammal is as dissimilar from that of a fish as their adult stages, no matter whether their differences are perceptible or not. This was the idea of the great old master Von Baer: The egg is as much a bird as is the hen.

Although perfectly true in a physiological sense, this is incorrect in this connection. Potentially the egg of one animal is as different from that of another as their adult forms, but morphologically they correspond. Morphology is not concerned with the "growth energies" of organisms, but only with their form and structure. A similar mistake was made by His in the quotation cited above, where he takes for an illustration of his views an animal which had lengthened its life over that of its ancestors. The logical deduction from such an example under the recapitulation theory would be that the last form should *die* at the end of each period, one, two, three years, etc., in order to recapitulate its ancestry, rather than that it *lives* one, two, three years to do so. The absurdity of this lies in the fact that length of days is not a morphological character. The recapitulation theory has nothing to do with physiology; it is purely a matter of morphology.

The degree of approximation between the young of a higher form and the adult of a present-day lower form of the same line depends upon the degree of specialization and divergence of the lower species from the main path of descent. It is usually recognized that most of the lowest and morphologically simplest organisms are highly specialized for some particular mode of life more or less different from the ancestral. This specialization nearly always carries with it some structural adaptations, but these may not obscure the ancestral characters. Thus *Marchantia* has evolved a chambered thallus highly differentiated, to adapt it at once to an aquatic substratum and aerial life, but it still retains a sporophyte perhaps very similar in some features to that of the ancestors of the higher plants at the liverwort stage. On the other hand, organisms are occasionally found which give every indication of being primitive. These are truly forms with arrested evolution. *Renfrewia* is an example; *Anthoceros* is another, less free from specialization but contrasting strongly

with Marchantia. Such primitive types are few and far between for obvious reasons: if an entire group advances rapidly it moves up bodily into a higher plane and leaves behind only such forms as stray into some byway of specialization, which specialization would be a bar to future progress except in the line upon which the form had entered. All unspecialized forms left behind in the advance of the race are likely to be displaced early in the struggle for existence because of their lack of particular adaptations. It is accordingly only in such environments as present no specialized demands upon their inhabitants that we may expect to find these primitive forms and it will be observed that to a large extent such is the case.

Wherever a form is found with simple unspecialized structure it becomes at once a problem to decide whether it is in reality primitive or a degenerate type. If there is no paleontological history to aid in the solution a conclusive answer to this question is often impossible. However, unless there is definite evidence of degeneration in vestigial structures or the like, as there is in many cases, for example the mistletoes; it is generally safe to assume that the present condition of the organism represents its highest attainment in the process of evolution. Degenerate forms usually manifest a high degree of fixity in their organizations and great variability is seldom found in such forms. It might be suggested that the apparently primitive structure of *Renfrewia* may be due to degeneration from a condition more highly differentiated. It possesses, however, no vestigial or unused organs, with the exception of the basal cone of the stipe. Every portion of the plant is functional. There are no peculiarities about its structure which mark it as different from the other kelps. On the contrary, its reproduction and its histology are similar to them. Its habitat, quiet water just below the tide mark, is exactly that which would be expected of the ancestors of the kelps before they acquired adaptations enabling them to endure the

heavy surf and the drying incident to living above the tide mark. At the same time it has such a high degree of variability in its whole structure that it is difficult to pick out characters sufficiently fixed to be of use in describing it. There seems to be no good reason to doubt its primitive position.

Taking all the evidence into consideration, it seems to the writer that we are bound to conclude that though organisms are subject to adaptation at any stage of their life cycles and may gradually cut out superfluous stages, yet, except as some such tendency has operated to change the heritage, the development of the individual does recapitulate the history of the race. The degree of correspondence of any individual cycle with its ancestral history is various in different cases but may be very close. Recapitulation must take place if there is any force which tends to make offspring like parent, if heredity is of any importance in moulding the forms of organisms. On the other hand, if there be any variability or transmutation of individuals in stages other than the adult end stages of their life cycles, the recapitulation can not be perfect, but must be marred at every stage where secondary change has taken place. The extent to which any individual will recapitulate its phylogeny must therefore depend on the balance maintained between these two forces in the given case. The value of a study of ontogeny for the taxonomist or phylogenist will depend altogether on the facts of the special case. In each case the evidence must be weighed before a conclusion can be reached. Ontogeny may be of greater or less worth in the attempt to build a rational system of nature. But variable as its utility may be in different cases, the recapitulation theory states a fundamental law of a tendency of the embryogeny and must be considered as one of the several interacting tendencies which together control the development of animals and plants.

COLUMBUS, O., August, 1908.

## LITERATURE

- No attempt is here made to list the voluminous literature devoted to discussions of the recapitulation theory. The more important papers have been thoroughly listed and summarized in many of the standard general works, *e. g.*, Montgomery.
- Barber, C. A. On the Structure and Development of the Bulb in *Laminaria bulbosa*. *Ann. Bot.*, 3, 41. 1899.
- Conklin, E. G. The Organization and Cell Lineage of the Ascidian Egg. *Jour. Acad. Nat. Sci. Philadelphia*, vol. 13. 1905.
- Frye, T. C. *Nereocystis lutkeana*. *Bot. Gaz.*, 42, 143-146, fig. 1. 1906.
- Gepp, A. and E. S. *Lessonia grandifolia*. *Jour. Bot.*, 43, 2. 1905.
- Grabendörfer. Zur Kenntnis der Tang. *Bot. Zeit.*, vol. 43. 1885.
- Griggs, R. F. *Renfrewia parvula*, New Kelp from Vancouver Island. *Postelsia*, 1906, 247-274, pls. 16-19. 1906.
- . *Cymathere*, a Kelp from the Western Coast. *O. Nat.*, 7, 89-96, pl. 7, fig. 1. 1907.
- Hooker, J. D. Flora Antartica, 2, t. 171, 167. 1844.
- Humphrey, J. E. On the Anatomy and Development of *Agarum turneri*. *Proc. Am. Acad.*, 23, 201. 1886.
- Kjellman, F. R. Laminariaceae in Pflanzenfamilien, 1<sup>2</sup>, 242-260. 1893.
- MacMillan, C. Observations on *Nereocystis*. *Bull. Torr. Club*, 26, 273-296, pls. 361-362. 1899.
- . Observations on *Lessonia*. *Bot. Gaz.*, 30, 318-334, pls. 19-20. 1900.
- . The Kelps of Juan de Fuca. *Postelsia*, 1901, 193-220, pls. 22-26. 1901.
- . Observations on Pterygophora. *Minn. Bot. Stud.*, 2, 723-741, pls. 57-62. 1902.
- Montgomery, T. H. The Analysis of Racial Descent in Animals. New York. 1906.
- Morgan, T. H. Evolution and Adaptation. New York. 1903.
- Oliver, F. W. On the Obliteration of the sieve tubes in the *Laminariae*. *Ann. Bot.*, 1, 95. 1887.
- Postels and Ruprecht. Illustrationes algarum. 1840.
- Ramaley, Francis. Observations on *Egregia Menziesii*. *Minn. Bot. Stud.*, 3, 1-9, pl. 1-4. 1903.
- Reinke, J. Studien zur vergleichende Entwicklungsgeschichte der Laminariaceen. Kiel. 1903.
- Saunders, D. A. Algae of the Harriman Alaska Expedition. *Proc. Wash. Acad. Sci.*, 3, 391-486, pls. 18-62. 1901.
- Schrader, Herman F. Observations on *Alaria nana*. *Minn. Bot. Stud.*, 3, 157-166, pl. 23-26. 1903.
- Setchell, W. A. Concerning the Life History of *Saccorhiza dermatodea*. *Proc. Am. Acad.*, 26, 177-217, pls. 1 and 2. 1891.
- . Classification and Geographical Distribution of the Laminariae. *Trans. Conn. Acad.*, 9, 333-375. 1893.
- . Notes on Kelps. *Erythrea*, 4, 41-48, pl. 1. 1896a.
- . *Eisenia arborea*. *Erythrea*, 4, 129-133, pl. 4; 155-162, pl. 5. 1896b.

- \_\_\_\_\_. The Elk Kelp. *Erythrea*, 4, 179-184, pl. 7. 1896c.  
\_\_\_\_\_. *Laminaria sessilis* in California. *Erythrea*, 5, 98. 1897.  
\_\_\_\_\_. Notes on Algae, I. *Zoe*, 5, 121-129. 1901.  
\_\_\_\_\_. Post Embryonal Stages of Laminariaceæ. *Univ. Cal. Pub. Bot.*, 2, 115-138, pls. 13-14. 1905a.  
\_\_\_\_\_. Regeneration among Kelps. *Ibid.*, pp. 139-168, pls. 15-17. 1905b.  
\_\_\_\_\_. Nereocystis and Pelagophyceus. *Bot. Gaz.*, 45, 125. 1908a.  
\_\_\_\_\_. Critical Notes on the Laminariaceæ. *Nuov Notarisia* 19: 90-101. *Rev. Jour. Roy. Mic. Soc.*, 1908, 474. 1908b.  
Setchell, W. A., and Gardiner, N. L. Algae of Northwestern North America. *Univ. Cal. Pub. Bot.*, 1, 165-418, pls. 17-27. 1903.  
Sykes, Miss M. G. Anatomy and Histology of Macrocytis and *Laminaria saccharina*. *Ann. Bot.*, 22, 291-325, pls. 19-21. 1908.  
Thuret. Recherches sur les Zoospores des Algues et les Antheridies des Cryptogames. *Ann. Sci. Nat.*, ser. 3, 14, 240, t. 30. 1850.  
DeToni, J. B. Sylloge Algarum, 3, 316-374. 1895.  
Wille, N. Beitr. Physiolog. Anatomie Laminariaceanum. *Univ. Fests. til. K. M. K. Oskar*, II, Anleitung Reggieringsjubilaet. 1897.  
Williams, J. L. Germination of the Zoospore in Laminariaceæ. *Nature*, 62, 613. 1900.  
Yendo, K. On Eisenia and Ecklonia. *Bot. Mag. Tokyo*, 16, 203. 1902.  
\_\_\_\_\_. Two new Marine Algae from Japan. *Ibid.*, 17, 99-104, pls. 2 and 3. 1903a.  
\_\_\_\_\_. *Hedophyllum spirale* sp. nov. *Ibid.*, 17, 165-173, pl. 6. 1903b.

## NOTES AND LITERATURE

### PLANT PHYLOGENY

**The Origin of the Archegoniates.**—There is in the theoretical discussion of plant evolution perhaps no gap which is more difficult to bridge than that between the thallophytes and the archegoniates, or more precisely that between the higher algae and the liverworts, mosses and ferns. The most recent discussion of this problem is by Schenck,<sup>1</sup> one of the authors of the "Lehrbuch der Botanik," who is convinced that the archegoniates arose from the Phaeophyceæ or brown algae.

A number of earlier writers have endeavored to relate the archegoniates to the Chlorophyceæ or green algae. This has generally been attempted through Coleochaete or Chara. Coleochaete has been a favorite type for the reason that its fruit, derived from the germination of the egg, is a globular multicellular structure somewhat resembling the sporophytes of the simpler liverworts in the order Ricciales. Allen, however, has reported that the phenomenon of chromosome reduction takes place during the germination of the egg and not at the end of this period of fructification, which clearly indicates that the latter development is not the homologue of a sporophyte. A comparison of the sexual organs of Coleochaete with those of the archegoniates presents further difficulties, for the antheridia and oogonia of Coleochaete are unicellular structures very different from the multicellular sexual organs of the archegoniates. The general morphology of Chara is somewhat moss-like, but in this form also the life history fails to present any evidence of an alternation of generations comparable to that of the archegoniates. Furthermore, the essentially unicellular structure of the oogonium (the protective investment of which is clearly a secondary feature) bears no fundamental resemblance to an archegonium, and its remarkable antheridium is unique among the sexual organs of plants.

The Rhodophyceæ or red algae have a highly developed sporophytic phase, but their diverse morphology as well as that of the

<sup>1</sup> Schenck, H. Ueber die Phylogenie der Archegoniaten und der Characeen. *Engler's Botan. Jahrbuchern.*, XLII, 1908.

gametophyte is so very different from anything present in the lower archegoniates that relationships between the two groups seem hardly possible. The work of Yamanouchi on *Polysiphonia* clearly indicates that the tetraspore mother cell when present is the seat of reduction mitoses terminating the sporophytic phase of the typical life history of the higher red algae. The sexual organs of the red algae are also far removed in structure from the sexual organs of the archegoniates.

Davis in 1903 first pointed out the resemblance of the archegonium and antheridium of the bryophytes to the plurilocular sporangium or gametangium of the brown algae, and advanced the view that the former arose from such a type of sexual organ as the latter through the differentiation of a sterile protective envelope around the gametes (in response to terrestrial life habits), and such sexual evolution as would give the highly developed condition of heterogamy present in the archegoniates. Davis, however, was unwilling to concede the probability of an origin of the archegoniates from the brown algae because of the great morphological differences between the two groups, but suggested that there may have been forms of green algae with plurilocular sporangia, now extinct, from which the bryophytes have been derived.

Schenck accepts the view of Davis that the sexual organs of the archegoniates are homologous with plurilocular gametangia and derived from them, but argues for a direct origin of the archegoniates from the brown algae. He gives an excellent series of figures, selected from various authors, which illustrates the principal forms of plurilocular sporangia and gametangia of the brown algae, and presents a similar series of figures of antheridia and archegonia of bryophytes and pteridophytes showing various points of resemblance in their structure and development. The resemblances are easily followed between the gametangia of the lower brown algae (*Phaeosporeæ*) and the sexual organs of mosses and most liverworts. However, there are difficulties when the antheridia and oogonia of *Dietyota*, the endogenous antheridia and sunken archegonia of *Anthoceros*, and the sunken sexual organs of certain eusporangiatae pteridophytes, *Lycopodium*, *Selaginella*, *Isoetes*, etc., are compared with plurilocular gametangia of brown algae in an attempt to derive in a direct manner the former from the latter. The reviewer agrees with Schenck that plurilocular sporangia and gametangia of the brown algae are in the same class of repro-

ductive organs with archegonia and antheridia, but would not be willing to go so far as to hold that the latter have been derived directly from the former.

There follows then in Schenck's paper an attempt to homologize the spore mother cell of the archegoniates with the tetrasporangium of the Dictyotaceæ, based on the fact that the mitoses in both cells are reduction divisions terminating the sporophytic phases of life histories with an alternation of generations. The endogenous formation of spore mother cells in the archegoniates is regarded as an ecological adaptation associated with terrestrial life habits. The analogy is perfectly clear, but it may well be questioned whether it suggests so close a relationship as to justify an homology, especially since reduction phenomena are now known for a number of unrelated groups of algae and fungi. The tetraspore mother cell of the red algae is probably in most forms also the seat of chromosome reduction terminating a sporophytic phase. The mitoses in the zygote of *Spirogyra* have recently been shown by Karsten to be reduction divisions, as has been suspected, and it is altogether probable that similar reduction mitoses will be found to occur with the germination of the eggs of *Oedogonium* and a number of other algae, and for certain phycemycetes as well. All of these cells in being the seat of reduction mitoses are analogous to the spore mother cells of archegoniates, but that would not warrant their being considered as homologous with the latter structures. There is, on the contrary, good reason to believe that in plants reduction phenomena became established as features in the life histories of a number of groups quite independently of one another, as the evidence indicates was also true of the processes of sexual evolution and the differentiation of sporophyte generations. Chromosome reduction as a physiological process seems to be a corollary of sexual nuclear fusions, but the cells concerned in the former are less likely to be homologous with one another than the cells concerned in the latter, since they are a part of a new phase which tends to become elaborated as the intercalated sporophytic generation. It is clear that a number of types of gametes throughout the plant kingdom are not homologous, and equally clear that several different forms of cells associated with chromosome reduction are not homologous.

Finally, Schenck compares the gametophytes and sporophytes of the archegoniates with the thalli of the brown algae, but it is doubtful whether he really strengthens his case. The resemblance of the gametophytes of thallose liverworts to band-shaped

forms of the brown algae is but superficial and does not extend to fundamental anatomical features. Indeed, both the brown algae and the bryophytes present so remarkable a variety of vegetative structure that it is very difficult to pick out types which may be held to be representative of the two groups. Schenck refers frequently to the conditions in the Dictyotales, but this assemblage is very far from being representative of the brown algae as a whole and stands rather as a group of very uncertain relationships. The simpler gametophytes of the pteridophytes may more readily be compared to the thalli of some of the lower brown algae, but they are very different from the higher forms where the sexual conditions are those of heterogamy, and, moreover, this simplicity in some types of pteridophytes is rather evidence of that general principle of plant evolution according to which the gametophytes become reduced in structure as the sporophytes attain higher levels of complexity. It is of course much more difficult to make comparisons between the sporophytes of the archegoniates and the thalli of the brown algae.

This portion of Schenck's paper appears to the reviewer to give very little support to his speculation and herein lies its principal weakness, for if the vegetative morphology of the brown algae is not suggestive of relationships to the archegoniates the resemblance between their sexual organs can scarcely alone carry much force, especially since the latter may with great probability be supposed to refer to older and more primitive conditions. The reviewer is still inclined to his opinion that there have probably existed groups of the green algae now extinct, the sexual organs of which were plurilocular gametangia, from which the archegoniates may have arisen. We have at present suggestions of such types in *Schizomeris*, *Stigeoclonium tenuie irregulare* and conditions occasionally found in *Draparnaldia* and *Chaetophora*. That such groups of extinct green algae may have originally had close relationships to the brown algae is quite possible.

In the last section of this paper Schenck discusses the origin of the Charales. Of especial interest is the suggestion that the puzzling antheridium of this group may be interpreted as a sorus of antheridial filaments developing endogenously and may be compared to the sori of plurilocular sporangia which are produced externally on the surface of certain brown algae. According to this view the globular male organ of the Charales is really

a complex of eight clusters of true antheridia in the form of filaments, and the entire structure constitutes a sorus-like structure in which the antheridial filaments arise endogenously. This conception has strong support in the abnormal conditions described by Ernst for *Chara syncarpa* where antheridial filaments were found developing externally from cells below the oogonium giving an hermaphrodite association of sexual organs. Schenek considers the Charales to be much more closely related to the brown algae than to the green, basing his views on the above considerations together with certain resemblances between their vegetative structure (characterized by nodal and internodal regions) and that of certain brown algae, Spermatochnus, Desmarestia, etc.

BRADLEY M. DAVIS.

#### HOLOTHURIANS

**Clark's The Apodous Holothurians.**<sup>1</sup>—Revisions of genera and larger groups require more painstaking care and research than most other forms of biological study, certain current opinion to the contrary, notwithstanding. Dr. Clark's memoir is a good example of a revision applied to a difficult group of animals. It is a well-executed and well-matured piece of work, and one which fulfills all reasonable expectations. It is easily the most important treatise that has ever been published upon the families Molpadiidae and Synaptidae.

The monograph is based upon a critical examination of about 2,200 specimens in the collection of the National Museum, and is divided into four parts. The classification of the two families is first discussed and a table of accepted genera, with type species, is given. Part II is an annotated list of the species in the collection of the National Museum, including descriptions of new genera and species. Part III contains an account of the Synaptidae, their morphology, embryology, physiology, ecology and taxiology, with keys to genera and species, and a short notice of each species, special attention being given to the geographical distribution. In Part IV, the Molpadiidae are treated in a similar manner. Of the thirteen plates, three are

<sup>1</sup> The Apodous Holothurians, A Monograph of the Synaptidae and Molpadiidae, Including a Report on the Representatives of these Families in the Collections of the United States National Museum. By Hubert Lyman Clark. Smithsonian Contributions to Knowledge, Part of Vol. XXXV, 231 pp., XIII plates, 1907 (issued early in 1908).

in color. The figures are intended to illustrate not only the new forms described, but also previously known species that have not been figured and some others, figures of which will be of service to the student. In a number of instances the nomenclature has been changed, and has been placed on as firm a basis as possible by the use of the generally accepted principles of the International Code. It will be seen that the monograph has a wider scope than a systematic revision, including as it does accounts of the anatomy, embryology and physiology.

The interesting account of the history of the classification of the two families is followed by an important consideration of the characters used in classification, and a discussion of the subfamilies and leading genera. Twenty-nine genera, of which 8 are new, are accepted, distributed as follows: Synaptinæ, 11 genera (2 new) comprising 60 species; Chiridotinæ, 7 genera (3 new) with 22 species; Myriotrochinæ, 3 genera, 6 species; Molpadiidæ, 8 genera (3 new and 1 new name) with 46 species. Dr. Clark has discovered that Ankyroderma is practically a juvenile condition of *Trochostoma*. As generally defined the former is distinguished from the latter by the presence of rosettes of racquet-shaped rods from the center of which there extends outward a conspicuous anchor. It was found, from a study of more than 350 specimens of these two genera, that the presence of anchors and rosettes of racquet-shaped rods can not be regarded as even a constant specific character. For example, small specimens of *Trochostoma intermedium* Ludwig with very thin skin are clearly Ankyroderma. Large specimens have a rather thick body wall and very numerous deep red or brown bodies in the skin, but no rosettes. The rosettes disintegrate into heaps of rounded colored bodies which differ from calcareous plates or particles in being chiefly phosphoric acid and iron. They are therefore quite unlike the ordinary calcerous deposits of holothurians, and are named "phosphatic deposits."

"As to the significance of these facts our knowledge is as yet too imperfect to draw any clear conclusions. Chemical analysis<sup>2</sup> of the

<sup>2</sup>The composition of these bodies is given as  $\text{FePO}_4 + 4\text{H}_2\text{O} = 66.2$ ,  $\text{Fe(OH)}_3 = 20.2$  and  $\text{CaCO}_3 = 6.4$ . There is also probably Mg present. "There is also reason to believe that the amount of  $\text{CaCO}_3$  is subject to much variation; probably when calcareous particles are first transformed into colored bodies,  $\text{CaCO}_3$  is the most important substance present, and

deposits shows that the colored bodies are radically different from the ordinary deposits in the skin. Both are possibly connected with the process of excretion; but why one should replace the other it is certainly hard to say. That the change is closely connected with the age of the individual seems to me almost certain, though it must be remembered that size in echinoderms is not a sure criterion of age. It is interesting to note that most of the species of Ankyroderma described have been less than 60 mm., while many of the Trochostomas range over 75" (p. 19).

The name *Trochostoma* antedates *Ankyroderma*, but both are synonyms of Cuvier's *Molpadia* (1817) which includes also *Haplodactyla* Grube (not Semper), as well as the long-discarded *Embolus* Selenka, and *Liosoma* Stimpson (not Brandt). In this enlarged genus *Molpadia*, twenty-seven species are recognized.

Some of the more important changes in the limits or names of genera, as well as certain new genera, will be noted. *Synapta* is monotypic and restricted to *S. maculata* Chamisso and Eysenhardt (*S. beselii* authors); *Oestergren's Chondroclea* is called by the older name *Synaptula*; *Leptosynapta* Verrill is reinstated for the *inhærens* group; *Synapta kefersteinii* is made the type of a new genus *Polyplectana*; the recently described *Opheodesoma* is accepted for the *Euapta glabra* group; the old species *Chiridota rufescens* is made the type of a new genus *Polycheira*; *Tæniogyrus* Semper, for *Chiridota australiana* Stimpson, is accepted as distinct from the later *Trochodata* Ludwig; *Chiridota japanica* v. Marenzeller is made the type of *Scolidota*, new; *Achirodota* is founded upon *Anapta inermis* Fisher, and *Toxodora* Verrill is reinstated. The most important change in the Molpadiidae has already been noted. *Haplodactyla* Semper 1868 (not Grube, 1840) is renamed *Aphelodactyla*, with five species. *Ceraplectana* and *Himastlephora* are two new genera, the former near *Molpadia*, the latter related to *Gephyrothuria* Koehler and Vaney.

It has occurred to the present reviewer that, had space permitted, a very useful feature would have been the insertion of a complete diagnosis under each species not described in Part II. It is not possible to include in keys all the positive characters of a species, nor is it always possible for the average as the color deepens, it decreases rapidly in amount. Apparently the caleum as well as the CO<sub>2</sub> is excreted as these changes take place" (p. 143). The presence of phosphatic deposits is limited to the Molpadiidae among echinoderms.

student to have access to original descriptions. No one is able to tell when an apparently useless character (from the systematist's standpoint) and therefore one invariably omitted from keys, may not assume prime importance in the light of unnamed material. The practical difficulty that one has in depending upon literature and concise revisions is this. By testimony of keys (and figures too) one may have a species very close to a named species, yet there may be present in the questionable form additional characters of which no mention is made in keys. If one has not access to the original or some later authentic description he is "up a stump." The writer has so often found himself in this undesirable position that he speaks with some feeling on the subject.

However, the lack of descriptions is partly compensated for by the excellent notes under "Remarks," and in some cases by the republication of figures. Students of the group have every reason to be grateful to Dr. Clark for a very timely and useful memoir, and one which has in several instances reduced to order what was seemingly hopeless chaos.

W. K. FISHER.

#### LEPIDOPTERA

**The Blue Butterflies of the Genus Celastrina.**—In the second volume of Mr. J. W. Tutt's "British Butterflies," recently published, is a most exhaustive account of the small blue butterflies represented in Europe by *Celastrina* (vel *Cyaniris*, vel *Lycæna*) *argiolus*, and in America by the common and widely distributed *C. pseudargiolus*. The latter insect has long attracted much attention, owing to its remarkable polymorphism, which has been elucidated very fully by Edwards and Seudder. Mr. Tutt has gone over the whole subject afresh, and with the assistance of Dr. T. A. Chapman and Mr. G. T. Bethune-Baker, has been able to reach a number of very interesting conclusions. It appears that *Celastrina* is essentially an old world type; found, or represented by close allies, in every one of the great zoological regions of the Eastern Hemisphere, though feebly represented in Australia and Africa. In America, it is represented by *C. pseudargiolus* and its subspecies, one of which extends as far south as Panama. An examination of the structural characters, especially the genitalia, shows that *pseudargiolus* is not in any way definitely separable from the palearctic *argiolus*, of which it must be considered a geographical race. It appears probable

that *C. argiolus* reached America in late Miocene times, and being able to live on a great variety of plants, spread widely, producing various local races. So long as it was restricted to temperate regions, it did not come to differ radically from the old world type; but the form *gozora* Boisduval, of the mountains of Mexico and Central America, is very striking in appearance. Even this last, however, has the genitalia and other structures of genuine *argiolus*. This case is especially instructive, because it indicates that an insect may spread very widely, invading regions with exceedingly diverse climates, and yet not change materially in the characters of the genitalic armature. When we remember how frequently allied species of insects, inhabiting the same or similar regions, are separable by genitalic characters, it seems that these are little or not at all connected with obvious environmental factors. To say that genitalic modifications are due to "mutation" does not really explain them; it remains to be shown, if that is possible, what it is that breaks down an established genitalic type, giving rise to new forms which rank as species. In the case of *Celastrina*, it is not to be assumed that its structural features are so immobile that they are incapable of modification. As a matter of fact, the numerous old world species are distinguished by the possession of very distinct genitalia, each very constant within specific limits. In Asia there are very distinct races, having precisely the structure of *C. argiolus*, and at the same time species exceedingly like *argiolus* superficially, but quite different in their genitalic appendages. From the standpoint of the natural selectionist, it may be remarked that there was nothing to be gained by genitalic differentiation in America, so long as only one species of *Celastrina* inhabited the country; and further, that the range of the insect, with all its local modifications, was practically continuous. It may be that in Asia (especially among the islands) distinct species arose, adapted to special food-plants and other conditions, and that whenever these spread so that their ranges overlapped, crossing—by throwing the organism out of gear with its environment—was injurious, and so tendencies to genitalic modification were preserved. If these arose by simultaneous mutation,<sup>1</sup> not by random scattering variation, they might in such a case lead to a pure differentiated race. Suggestions of this sort are of course to be taken with an adequate supply of salt, but they have their use as stimulating enquiry.

<sup>1</sup> Or, perhaps, were already present as Mendelian recessives?

Some years ago, in an address before the Entomological Society of London, Professor Poulton raised the question whether the ability to mate successfully was not after all something maintained by rigid natural selection; and if I remember his argument correctly (I do not possess a copy of his paper), he believed that differences in the sexual organs might be expected to arise whenever selection ceased to operate. Since that time Tower has produced striking evidence of the small amount of divergence which suffices to throw an organism (in his instances beetles) out of the race. In this connection it may also be remarked that the singular fertility between different races of men, dogs, cattle, etc.,—many of these differing exceedingly in many characters of color and form—may be attributed to the effects of natural selection. The purest breeds of dogs, and no doubt the best established races of men, are after all great mongrels; and in the course of time no doubt interracial infertility would be absolutely discriminated against. However active the imagination may be in picturing causes and effects, it can but pause before such cases of genitalic modification as are described by Dr. J. B. Smith in his revision of the moths of the genus Homoptera and its immediate allies, just published by the U. S. National Museum. In some of these moths the sexual organs are extremely asymmetrical. "In the males the asymmetry is between the harpes of the two sides, which in extreme cases are totally dissimilar, with processes on one side for which there is no counterpart on the other, and which are rarely entirely alike. The sheath of the penis or intromittent organ is always more or less curved or bent, or even hooked, and this structure is directly correlated to the differences found in the female." These peculiarities are all figured most carefully.

T. D. A. COCKERELL.

#### VERTEBRATE PALEONTOLOGY

**The Lysorophidæ.**—In 1875 Dr. J. C. Winslow, of Danville, Illinois, a local collector of fossils, discovered, at "Horseshoe Bend," on Salt Fork, on the Tate farm, some two miles south of Oakwood, in Vermilion County, Illinois, some bones which he sent to Professor Cope for identification. Later on the work of exploration at this place was taken up by Mr. W. F. E. Gurley and his collection was transferred to the University of

Chicago, where it now is. In 1877 Cope published a description of several forms from among the remains collected at "Horse-shoe Bend" among which was the form *Lysorophus tricarinatus*, based on three vertebrae, which Cope took to be of reptilian nature. From the fact that the bones were very similar to some found in the Texas Permian, Cope concluded that the Illinois deposit was likewise Permian; and such it is usually regarded. From the discovery of a similar deposit in Pennsylvania by Raymond<sup>1</sup> it seems more probable that the deposit in Illinois is Pennsylvanian, as is the deposit in Pennsylvania.

In the summer of 1907 Dr. S. W. Williston sent the writer to the Illinois locality for the purpose of settling the stratigraphy, if possible, and to secure more material to illustrate the forms which are so meagerly known. The deposit was found to be already exhausted and after a month's work scarcely a handful of bones was secured. The stratigraphy was almost impossible of determination, though Dr. Stuart Weller, who visited the locality, was of the opinion that the circumstantial evidence was very strong in favor of its being upper Pennsylvanian. Since the discovery of similar deposits in Pennsylvania of undoubtedly Pennsylvanian age it seems no longer necessary to doubt the Carboniferous age of these Illinois deposits. In 1902 in "Contributions from Walker Museum, Vol. I, p. 45," Case announced the discovery of typical vertebrae of the *Lysorophus tricarinatus* type from the Permian of Texas. Last June Case<sup>2</sup> described the skull of the *Lysorophus tricarinatus* and came to the conclusion that the form was an amphibian. Later in the summer and almost simultaneously papers by Broili<sup>3</sup> and Williston<sup>4</sup> appeared on the same subject. Broili emphatically denied the amphibian nature of *Lysorophus* and Williston proved conclusively that the form is not only an amphibian, but is even allied to the modern Urodela. Broili reaches the most astonishing conclusion that *Lysorophus* "erscheint daher nach den in der Systematik geltenden Grundsätzen für richtiger, . . . zu den Lacertiliern zu stellen."

Williston shows very conclusively that the form is an undoubted amphibian and gives the following characters to support his views: skull pointed with no evidence of orbits, paired

<sup>1</sup> *Science*, N. S., Vol. XXVI, No. 676.

<sup>2</sup> *Bull. Amer. Mus. Nat. Hist.*, Vol. XXIV, p. 531.

<sup>3</sup> Broili, *Anat. Anz.*, Bd. XXXIII, No. 11/12.

<sup>4</sup> Williston, *Biol. Bull.*, Vol. XV, No. 5.

epiotes present, supraoccipital unpaired, condyle unossified, *branchial apparatus well developed*, vertebral column slender, limbs apparently absent, ribs long, somewhat curved and flat, neurocentral. Williston concludes:

"The only aberrant character to distinguish *Lysorophus* from the Urodeles is the long and rather broad ribs, unknown among these modern animals or their possible ancestors, the Branchiosauria. It is, however, very evident that the earliest ancestors of both these groups must have long ribs, and their persistence in *Lysorophus* would be nothing remarkable."

But why need we conclude that the early ancestors of the Amphibia must have had long ribs? There is no geological evidence of such, and the oldest known branchiosaurian, *Micrerpeton caudatum* Moodie from the middle Pennsylvanian certainly possesses very short ribs. The animals associated in the Carboniferous with the Branchiosauria, as a rule, possess long ribs, but do we need to infer that the Branchiosauria and the Microsauria had the same ancestry?

In all the long stretch of geological time there has never existed a branchiosaurian nor a true urodele which had long ribs, and so far, aside from the frogs found in the Tertiary, these are the only true amphibians known in the fossil state. It is exceedingly incongruous to class the Microsauria and Branchiosauria in the same order Stegocephala. Their organization is totally different. To be sure, the long ribs in *Lysorophus* might have developed secondarily as Williston suggests, but why do we need to assume even this when among the modern Gymnophiona we find long ribs and every other character which is present in the *Lysorophus*? It is also possible that the Gymnophiona are true Caudata, in which case there would be no distinction and it may be that *Lysorophus* will be of great assistance in bridging over this gap between the Caudata and the Gymnophiona.

Certain it is that the form is a most interesting discovery and one of the most important in the phylogeny of the extinct Amphibia in many years. I quote herewith from a letter to Dr. Williston from Dr. Broom which the former was so kind as to send me during the course of our correspondence on the subject:

"The skull (of *Lysorophus*) is to my mind undoubtedly Urodele and singularly like that of *Amphiuma* which I believe to be the nearest living ally. I am convinced that it is not a Gymnophionid . . ."

Here are then three various points of view offered for study—one, of Broili, that the form is a lacertian; two, that of Williston and Broom, that the form is a member of the true Caudata; three, the suggestion offered here that the form may be one of the Gymnophiona. In further support of the view of the gymnophionid character of the form is the snake-like character assumed by *Lysorophus*. Case has noted that the vertebral column is usually coiled where there is any considerable portion of it preserved and Dr. Williston remarked to the writer of the same fact which he had observed in the field while in Texas the past summer. The palate structure of the *Lysorophus* is against the idea of the form being a member of the Gymnophiona, at least so far as we know the palate; further knowledge of this structure will undoubtedly solve the problem.

Further study of the form will also reveal other facts as to its anatomy and we are hoping to hear much from the recent collections of Drs. Williston and Case from the Texas Permian.

**Stegocephala.**—In an endeavor to reach some definite conclusions in regard to the correct classification of the extinct Amphibia, investigators all over the world are issuing contributions on various phases of the subject. One of the more recent advances is a study of the vertebræ of the Carboniferous forms by Hugo Schwarz,<sup>1</sup> of Griefswald, Germany. He has studied the exact characters of the vertebræ of forms from the coal mines of Linton, Ohio, of which there are specimens preserved in Berlin and in Griefswald, and also specimens from Nürschan bei Pilsen. The work was done under the advice of Dr. Otto Jaekel and the paper shows a strong bias of Jaekel's views.

The methods of study adopted by Schwarz are the same as those proposed by Jaekel five years ago. The specimen is removed from the soft coal, in which it is imbedded, by chemicals and by mechanical means and an impression is made of the mold by wax, plaster or guttapercha. While most of Jaekel's results show that the methods have some advantages, yet it is to be doubted if they are the best in all cases. The interpretation of the material is a puzzle at the best, and when the elements are disturbed it is often very difficult to form any idea of their nature. Jaekel experienced this especially in his discovery of the "perisquamosal" in *Diceratosaurus*, a structure which does not exist in other species of this genus and was probably due

<sup>1</sup> *Beiträge zur Paleon. und Geol., Oesterreich-ungarns*, Bl. XXI.

to breakage in the form which Jaekel studied. Schwarz has, on the other hand, obtained excellent results, and his descriptions of the vertebre of the various forms will be of great service to the student even though his conclusions are not accepted.

A new family "Ophiderpetontidae" is proposed to include the genera Ophiderpeton and Thyrsidium, the former of which was included in Lydekker's Dolichosomatidae. The family characters are solely those exhibited by the ribs and vertebrae. Under the heading of Ophiderpeton the author rediscusses the question of the "Kammplatten" and dismisses the subject with the remark "dass sie nichts mit den Stegocephalen zu tun haben." Herein he has committed an error, for Fritsch has distinctly figured<sup>2</sup> a nearly complete specimen of *Ophiderpeton persuadens* Fr. with the "Kammplatten" in place near the cloacal region of the animal. The whole question of the "Kammplatten" has recently<sup>3</sup> been reviewed by the present writer. There is a great deal of uncertainty as to what the true nature of the "Kammplatten" really is. That they do occur in selachians as stated by Fritsch<sup>4</sup> does not at all imply that they may not also occur in Ophiderpeton, and they certainly do occur here if Fritsch has correctly interpreted his specimen.

Schwarz adopts the two suborders Aistopoda and Microsauria for the "Holospondylen Stegocephalen," but does not seem to understand the differences which exist between these two sub-orders, and especially is this true when he includes the Ptyoniidae in the Microsauria, since Ptyonius and its allies are typical members of the group Aistopoda. There is really but little difference between the groups Aistopoda and the Microsauria structurally, and, as Schwarz suggests, they undoubtedly arose from the same stem much as did the lizards and snakes, but they are just as distinctly members of different groups as are the Lacertilia and Ophidia. No form is more typically an aistopod than the Ptyonius. The subordinal characters are found in the vertebrae, in the lack of limbs, the elongation of the body and especially in the attenuation of the skull with its concomitant structural differences.

The final conclusion attained by the author is that, with Jaekel, he would divide the Stegocephala into two groups, the

<sup>2</sup> Fritsch, 1901, "Fauna der Gaskohle," Supplement, Vol. IV, p. 89.

<sup>3</sup> Biol. Bulletin, Vol. XIV, No. 4, 1908.

<sup>4</sup> Sitzungsberichte der Boh. Gesell., 1905.

temnospondylous groups and the holospondylous group. In the first group he would place all the forms which possess rhachitomous, embolomerous and stereospondylous vertebræ, and in the second group the forms which are usually known as Aistopoda and Microsauria. He evidently excludes the Branchiosauria from the Stegocephala proper, in which the present writer heartily agrees.

The contribution is a distinct advance in the knowledge of the forms described and it is to be hoped that we may have more information on the European forms which have been only too little studied and described.

**The Cotylosauria.**—The anatomy of this peculiar group of reptiles has been further elucidated by the recent studies of Williston<sup>1</sup> and Broili.<sup>2</sup> Williston restudied the form first described by Cope under the name of *Parioticus incisivus*. The University of Chicago possesses a nearly complete skeleton of this form and from his studies of this specimen Williston reached the conclusion that the form belongs rather in the genus *Labidosaurus* and is a typical cotylosaurian. He has given detailed figures of the anatomy of the various portions of the skeleton and a restoration of the form in so far as it is known. Broili has also given a restoration of a species of *Labidosaurus*, *L. hamatus*. He has mounted the entire skeleton free. This was impossible in the case of the specimen studied by Williston. Broili's restoration is a welcome addition to the knowledge of the Cotylosauria, although I am sure the animal, were he alive, would prefer not to have such an awkward sway in his vertebral column. One of the peculiar things about the Cotylosauria is the absence of lateral line canals which might be expected to be present from the close resemblance in their organization to the Stereospondyli, in which these canals are well developed. Dr. Williston searched carefully for the canals, but without success. The presence or absence of the canals may, at some future time, be one of the chief distinguishing characters between the forms which we call reptilian and those we call amphibian.

As a postscript to his article on *Lysorophus*<sup>3</sup> Williston has figured and described the ventral ribs of *Labidosaurus incisivus*.

<sup>1</sup> *Journ. Geol.*, Vol. XVI, No. 2, 1908.

<sup>2</sup> *Zeit. Deutsch. geol. Gesell.*, Bd. 60, H. 1, 1908.

<sup>3</sup> *Biol. Bull.*, Vol. XV, No. 5, 1908.

From the presence of these small abdominal ribs Williston concludes that: "This character adds another evidence of the relationship between the Procolophonia and Labidosaurus, and destroys its value as a group distinction." Broili, on the other hand, sees closer relationship between the Cotylosauria and the Stegocephala.

**The Oldest Known Reptile.**<sup>1</sup>—Dr. S. W. Williston has recently redescribed the type specimen of the oldest known reptile. This form, which Williston proposes to call *Isodectes copei* sp. nov., was doubtfully referred by Cope to the genus *Tuditianus*, but subsequently he referred it to the Texas genus *Isodectes*. It certainly does not belong in *Tuditianus*, and while there is no positive evidence that the form belongs in the genus *Isodectes* it seems well to leave it there until the characters of *Isodectes* are better known. The specimen is No. 4457 of the U. S. National Museum. It is preserved in a block of soft coal from the Linton mines of Ohio which have furnished nearly all of the remains of Carboniferous quadrupeds yet known in North America. The Linton mines were undoubtedly located well down in the Pennsylvanian and there has not yet been described a reptile from a lower horizon. The affinities of the form are doubtful though its close relationship to the Microsauria is well established. The intercentral attachment of the ribs and the apparent loss of the hypocentra in *Isodectes copei*, may require a revision of the theory of the formation of the reptilian vertebrae. The absence of abdominal ribs in this form is significant in the light of the recent discussions of the relationships of the early reptiles.

**The Age of the Gaskohle.**—Students of vertebrates the world over have become accustomed to accepting Fritsch's interpretation of the age of the Gaskohle of Bohemia as Permian. It is with some surprise, though not a little gratification, to note that through the recent studies of European geologists and paleontologists the deposits in Bohemia are now being regarded as Upper Carboniferous. The facts and arguments are well set forth by Broili<sup>1</sup> in a recent discussion on *Sclerocephalus*. Besides thus adding to the stratification of the forms of Amphibia the new fact is thus brought out that the large form *Sclero-*

<sup>1</sup>*Journ. Geol.*, Vol. XVI, No. 5.

<sup>1</sup>*Jahrbuch d. K. K. Geol. Reichsan.*, Bd. LVIII, H. I.

cephalus, which is possibly temnospondylous, occurs first in the Upper Carboniferous. A close parallel of this is found in the discovery of *Eryops* by Case<sup>2</sup> in the Upper Pennsylvanian of Pennsylvania. The progress of discovery is thus forcing further and further back into geological time the origin of the Amphibia. We now know nearly all of the types of the so-called Stegocephala from the Carboniferous and some of them occur well down in the system.

The results given by Broili are based in large part on the geological and paleobotanical studies of Weithofer and Feistmantel. The report is a lengthy one and occupies some twenty pages, including lists of the vertebrates and the plants which occur in the "Gaskohle schichten."

**Bison occidentalis.**—In the last issue of the *Kansas University Science Bulletin* Dr. C. E. McClung<sup>1</sup> has described and figured a mounted skeleton of *Bison occidentalis*. This specimen was first noted by Williston in 1902.<sup>2</sup> It was later<sup>3</sup> described by Stewart as belonging to the species *B. antiquus* which is now assigned to *B. occidentalis*. The skeleton has only recently been mounted by Mr. H. T. Martin and is noteworthy as being the only mounted skeleton of a Pleistocene bison. The specimen is further noteworthy because of an arrow point found under the right scapula as if it had been imbedded in the flesh before death. From his study of the mounted skeleton Dr. McClung reaches the conclusion that the extinct species was of a more cursorial type than is the modern *Bison bison*.

**Nectosaurus.**—Three years ago Dr. J. C. Merriam<sup>1</sup> gave to the world a memoir on a peculiar group of marine reptiles which he had discovered in the Triassic rocks of California and to which he gave the appropriate name of Thalattosauria. He has recently<sup>2</sup> added to the knowledge of the Thalattosauria by additional notes on the anatomy of Nectosaurus. From his recent studies Merriam concludes that Nectosaurus is a shore dwelling form and the evidence seems strong enough to warrant

<sup>1</sup> *Annals Carnegie Museum*, Vol. IV, No. III-IV, 1908.

<sup>2</sup> *Kans. Univ. Sci. Bull.*, Vol. IV, No. 10.

<sup>3</sup> *Amer. Geol.*, Vol. XXX, International Congress of Americanists, 1902.

<sup>4</sup> *Kansas Univ. Quarterly*, 1897.

<sup>5</sup> *Memoirs Calif. Acad. Science*, Vol. V, No. 1.

<sup>6</sup> *University of California Publications, Geology*, Vol. 5, No. 13.

the conclusion that *Nectosaurus* is not a young form of *Thalattosaurus* as the author suspected when he wrote his memoir on the Thalattosauria.

**Callibrachion.**—F. von Huene has restudied<sup>1</sup> the original specimen of *Callibrachion gaudryi* Boule and Glan, from the figure published in *Mem. Soc. d'Hist. Nat. d'Autun*, 1893, Taf. 3, and has republished this figure as a page plate. He was led to this study by the fact that the three incongruous characters of coronoid process of the mandible, opisthocelous cervicals and the presence of only about 20 presacral vertebrae being assigned to the form and on these characters it had been assigned to the Protorosauria by earlier authors and later to the Pelycosauria and here it is placed by Case in his "Revision of the Pelycosauria." Huene comes to the conclusion that the form is a close relative of Paleohatteria

"Hieraus folgt, dass Callibrachion nicht zu den Pelycosaurien gehören kann, sondern sich Paleohatteria sehr nahe anschliesst und wohl als einer ihrer direkten Nachkommen aufzufassen ist."

He is then of the opinion that the earlier authors were right in assigning Callibrachion to the Protorosauria. There are 23 presacral vertebrae which are amphiecelous as in the Paleohatteria. The coronoid process is wanting in Callibrachion.

ROY L. MOODIE.

#### PARASITOLOGY

The Sleeping Sickness Bureau, recently established in London, has begun the publication of a bulletin. The first number (October, 1908) is devoted to a review of the "Chemotherapy of Trypanosomiasis." The treatment of trypanosomiasis in man, the biological accommodation of trypanosomes to chemotherapeutic agents and the treatment of experimental animals are considered in succession. A bibliography of some 200 titles concludes the number. Future issues of the bulletin will include all the current literature of trypanosomiasis.

The following items excerpted from the summary of this mass of experimental material are of primary biologic interest. The use of any trypanocide by itself can not be justified. Combined therapy has the advantage that each drug can be used in smaller doses. The alternation of trypanocidal agents avoids the habituation of the parasites to a single remedy which has been thor-

<sup>1</sup> *Centralblatt für Mineral. Geol. Paleontologie*, 1908, No. 17.

oughly demonstrated through laboratory experiments. A second paper deals with the medical results of segregation camps and of chemical therapy in Uganda.

In the Huxley lecture, delivered at Charing Cross Hospital, October 1, 1908, Sir Patrick Manson, speaking on "Recent Advances in Science and their Bearing on Medicine and Surgery," discussed some points of great interest to biologists. At the start he noted the propriety of this theme for a Huxley lecture since the successful study of tropical diseases both depends on the use of those methods so consistently and powerfully employed by that great master of natural science, and also deals primarily with animal organisms, protozoa and helminthes, as disease producers and their special vectors, commonly arthropods, while bacteriology is relegated to a secondary place. In the study or teaching of tropical medicine this fact must be recognized by the addition to each staff of a protozoologist, a helminthologist, and an arthropodologist with suitable library and laboratory facilities. After presenting a synoptic table which outlines the principal tropical diseases with their causal and intermediary agents, the lecturer proceeds to discuss the appropriateness and value of biological theories in scientific advance with special reference to this field. Certain blood-inhabiting protozoa require a second host as a medium for a sexual cycle, as for instance the malarial plasmodium makes use of the mosquito. Is this to be regarded as a general law applicable to all such protozoa? The answer to this question is of fundamental importance in practical medicine as well as of intense interest to the biologist. The case of the sleeping sickness trypanosome will serve as an example for testing the problem.

The chief argument in favor of such a law is to be found in analogy, and though it must be used with caution the evidence in this case is distinctly favorable. All animals appear to require periodic sexual changes, and in other protozoa a sexual cycle necessarily interrupts the periods of asexual reproduction if the existence of the species is to be prolonged beyond narrow limits. In many cases where the existence of such a sexual cycle had long been denied it has been demonstrated by more intensive study. So highly developed a form as the trypanosome can hardly be an exception to this rule. By analogy such a stage would be found outside the human body and probably in the appropriate carrier of the disease, the tsetse fly.

On the other hand, four arguments have been brought forward against the acceptance of such a law: (1) No such sexual phase has yet been demonstrated in any trypanosome. The history of science gives scant weight to such negative evidence, especially when one considers the minuteness of the organism and the refractory character of the object studied, the tsetse fly. (2) The sexual phase of the trypanosome may be passed in the vertebrate blood and thus the tsetse fly be a mere mechanical carrier. There is, however, no evidence favorable to this view, either in observation or by analogy. (3) The successful inoculation of the trypanosomes through a long series of vertebrate hosts has been held to indicate that a sexual cycle is unnecessary. Yet similar laboratory transfer has been practised with the malarial plasmodium, for instance, though such a sexual cycle in the mosquito is demonstrated beyond all question. (4) An insect intermediary is apparently unnecessary in one trypanosome, that which causes dourine or mal du coit in horses, and therefore is not a biological necessity in any other species of trypanosome. This Sir Patrick Manson regards as the most formidable argument yet advanced against the law under discussion, but does not consider it as final. He devotes much space to the consideration of details in the case and the presentation of an alternative hypothesis which is too involved to reproduce in abstract. While the discussion presents many points of interest, yet the entire absence of experimental evidence in its support leaves this view as at present a bare working hypothesis. It may be added further that even the total rejection of this hypothesis does not necessitate the adaption of the view it combats. Much further investigation is needed before one can say with any confidence how the evidently exceptional case of the dourine trypanosome is to be explained. He concludes:

"I hold, therefore, that the existence of a sexual phase in the sleeping-sickness trypanosome, *T. gambiense*, and other trypanosomes, is more than probable, and that it has not been disproved; that the argument founded on the natural direct communicability of dourine in the apparent absence of an insect intermediary for its germ, *T. equiperdum*, is not valid; and that the evidence hitherto adduced is distinctly in favor of a law to the effect that blood-haunting protozoa having arthropod vectors require, and make use of, these vectors for necessary sexual development. Why the sexual stage of these parasites is passed in the arthropod, and not in the vertebrate, I cannot explain,

any more than I can explain the contrary arrangement which obtains in the blood-haunting nematodes, the sexual stage in their case being passed in the vertebrate host, the asexual in the insect.

"I have no doubt, while listening to these remarks, it has occurred to some of you, as it has often occurred to me, that the principles I have endeavored to express have a wider application than that which I have directly indicated, that our disease germs and our ectozoa—insignificant though the latter appear to be—are correlated more frequently than is generally suspected; that, in fact, there is a necessary relationship between them."

HENRY B. WARD.

#### EXPLORATION

**Camp-fires on Desert and Lava.**<sup>1</sup>—Lovers of outdoor life in the far distant west will be delighted on opening W. T. Hornaday's recent work, "Camp-fires on Desert and Lava," to observe, on the back of the half title page, a figure of the omnipresent Eleodes in very characteristic attitude. This little black creature by his position seems to be pointing us heavenward, but far from it. He is ever ready to present us with a drop of sticky brown fluid which has a horrible odor and whose stain will withstand the strongest soaps. The beetle forms a fitting introduction to the delightful account which follows.

The author needs no introduction to the reading public nor to the zoologist. To the one he is already well known by his previous volumes and to the other by his connection with the National Museum and with the New York Zoological Park as well as by his scientific writings, not the least important of which is his "Extermination of the American Bison," published in 1889. Mr. Hornaday is an enthusiastic collector and observer. All those who follow him into the Pinacate region, described in the present work, will never regret it.

On our present maps the region visited by Mr. Hornaday and his friends is variously located; suffice it to say that it is in the northwestern part of Mexico and not many miles from the Gulf of California. The region was attractive for several reasons, among which was the one that it had never been explored by any scientist or if it had there was no record of it. Other reasons which attracted the party to the region were the possible presence of big game and for Dr. MacDougal, who originated the plan, there were untold new plants, of a type very interesting to him, to be discovered. Dr. D. T. MacDougal made

<sup>1</sup> William T. Hornaday, *Camp-fires on Desert and Lava*. Illustrated. Charles Scribner's Sons, New York, 1908.

up the expedition under the auspices of the Carnegie Institution to extend his researches on the desert flora, and on the journey down to Mexico the author tells us of their visit to the famous "Desert Botanical Garden" near Tucson, Arizona, of which Dr. MacDougal was one of the originators, and from which point the expedition outfitted.

To those who have explored in the semi-arid regions of the western states the account given by Mr. Hornaday of their cross-country trip, recalls many familiar scenes. The cold mornings, the blistering hot days and the delightfully cool evenings are all features of a trip into the desert regions of the west. All the scenes along the trail are brought before the reader by pictures from pen and camera. The colored photographs are especially striking. Botanists will find an interesting account of the desert flora of southern Arizona and northern Mexico and the zoologist will find a description of the few animals which can manage to exist in this forlorn region. There is ever an attraction in the desert; even the barrenness of things and the apparent absence of all life make what little life there is all the more interesting.

On the arrival of the party near the Pinacate region a long camp was made and short exploring trips were conducted from the main camp. This was made necessary from the fact that the character of the country forbade further progress with the wagons. At this place also occurred the only "row" of the trip. Old campers know how painful it is to have a "row" on in camp. It is painful for those immediately concerned and for those who have to witness it. Their stay at Pinacate was of some length and full of success. They secured much big game and saw many interesting plants and photographed many new plants and craters which abounded there. The most abundant large mammal was the mountain sheep, *Ovis canadensis*. The author gives, in chapter XXIV, a discussion of the geographical distribution of the mountain sheep and also the synonymy of the species and subspecies of this interesting group of ungulates.

The last two chapters tell of the flight from Pinacate and the return to civilization. "The reaction from the steady and severe rush of the trip left us limp and spiritless, and it was four full days ere one member of the party began to feel quite like himself again." Thus ends the account of this unique exploring trip into the unknown regions of the southwest.

ROY L. MOODIE.

